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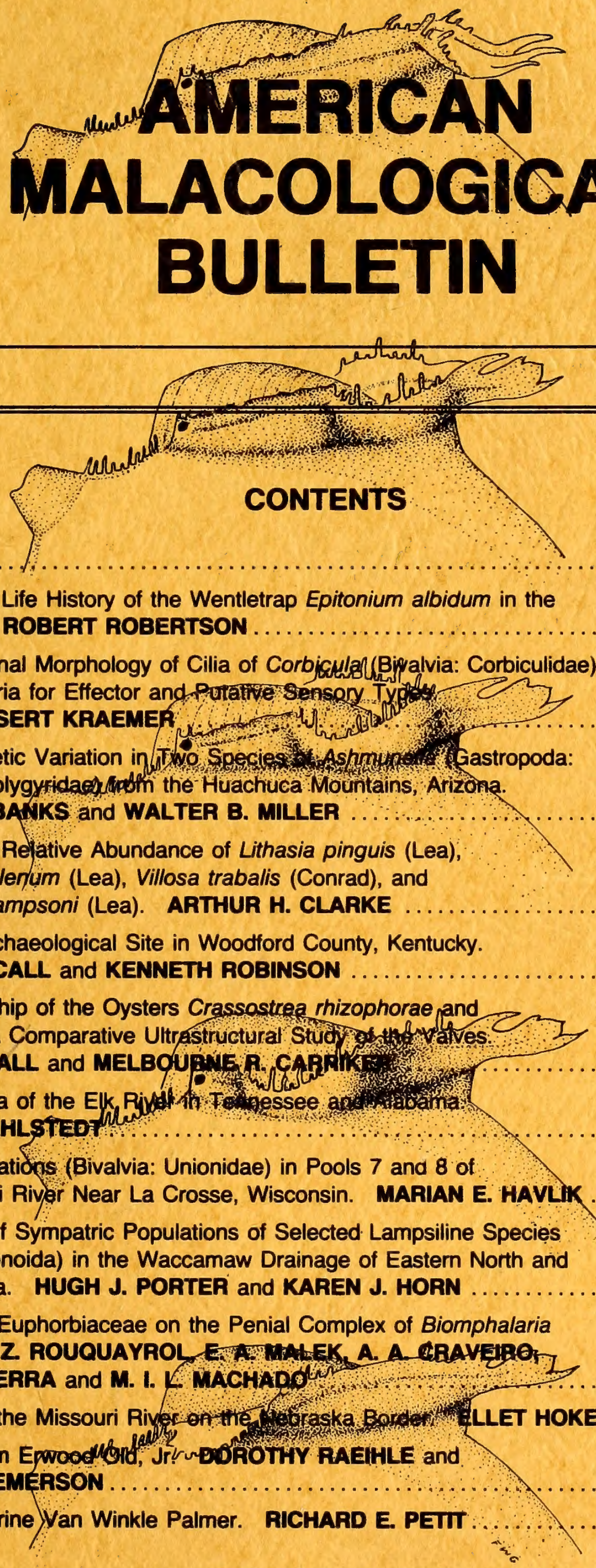

AMERICAN MALACOLOGICAL BULLETIN

VOLUME 1 JULY 1983

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Cover underprint: Sequential drawings of mantle flaps of a living, gravid female freshwater mussel, *Lampsilis ventricosa* (Barnes), during spawning behavior. Mantle flap movements are initiated as a pair of pulses near the "tail" ends of the flaps and move toward the "tail" thrusting the "eyespot" ends (located near the branchial siphon) outward and down. Glochidia-charged water tubes of marsupial gills protrude between mantle flaps during flapping behavior. (Drawings by Frances Waite Gibson, from Kraemer, 1970).

Supersedes;

THE AMERICAN MALACOLOGICAL BULLETIN (formerly the Bulletin of the American Malacological Union) is the official journal publication of the American Malacological Union.

AMER. MALAC. BULL. 1
May 1983

EDITORIAL COMMENT

Since its inception, the American Malacological Union has been a constantly evolving society. At times the AMU has progressed with gradual, almost imperceptible steps. At other times the society has bounded forward. The development of a new journal format, basically a new malacological outlet in the form of the **American Malacological Bulletin,** is one of those saltatory steps prompted by the continued growth of the American Malacological Union.

Several stimuli inspire the production of this revised publication. The need for additional malacological journals is obvious as interest and research in molluscan studies continues to mount. The persistently high quality research reported in AMU Bulletins deserve an accentuated and expanded AMU journal. The firm footing already secured by the **Bulletin of the American Malacological Union** has set the stage for the present metamorphosis. The new format calls for acceptance of high quality, well reviewed articles on any aspect of molluscan research. This is a change from the previous format of the **Bulletin** that served only to report meeting papers and abstracts. With this change, that is expanding the format to include "outside" papers, we start a new phase of growth in the AMU and make available a new periodical for submission of malacological manuscripts. The significance of this change is noted by the production of a new volume number, volume 1, under a new name, the **American Malacological Bulletin.** The name has been designed to reflect past contributions of the **Bulletin of the AMU** and to reveal the important change in status of the journal.

This first volume of the **American Malacological Bulletin** includes 1982 meeting papers and abstracts, as well as solicited papers. In the near future we will go to two numbers per volume per year; one partially devoted to meeting reports, and both containing additional high quality malacological papers. The new **American Malacological Bulletin** has been launched to fill the needs of molluscan researchers for an additional, much needed forum. We hope to see the **Bulletin** grow and develop into a major source for archiving malacological information and act as a foundation for stimulating additional malacological research.

The Editor

OBSERVATIONS ON THE LIFE HISTORY OF THE WENTLETRAP *EPITONIUM ALBIDUM* IN THE WEST INDIES

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ABSTRACT

In the Bahama Islands, British Virgin Islands and Barbados, the wentletrap *Epitonium albidum* (Orbigny, 1842) lives in shallow water with the actiniarian sea anemone *Stichodactyla helianthus* (Ellis, 1768), on which it feeds. Depending on the locality, from 11 to 100% of the anemones examined had wentletraps with them. The wentletraps usually live next to the anemone's column under the edge of the broad oral disc. When wentletraps were present, from 1 to ca. 39 individuals were found with single anemones, mainly those with sand around the column. The *Epitonium* commonly hides in the sand and uses it to agglutinate its egg capsules. Movement from one anemone to another is frequent.

Wentletraps were often observed everting their acrembolic proboscises and ingesting part or all of a *Stichodactyla* tentacle from near the edge of the oral disc; the column was also seen to be attacked, and *Stichodactyla* mucus is ingested occasionally.

The spermatozeugmata are grossly similar in morphology to those of epitoniids described and illustrated previously. Spermatozeugmata do not "swim" from a male to a female. Instead, pseudocopulation (juxtaposition of a male with a female) apparently occurs, resulting in spermatozeugmata entering the female's mantle cavity via ciliary water currents. The eupyrene spermatozoa seem to have an opisthobranch-like spiral keel on the middle piece.

Egg capsules resemble those described for other epitoniids, but are species-specific in morphology. The capsules are connected one to another by an elastic mucous thread coming from the pedal mucous pore. Small females lay small capsules (0.7 mm long), while larger females lay larger ones (1.7 mm or more long). Capsules 0.7 mm long contain many fewer eggs (mean: 32) than do those 1.7 mm long (mean: 137). In the laboratory, 331 egg capsules were laid by one 12.6 mm animal in 21 days (15.8/day). A 16 mm animal perhaps has laid about 200,000 eggs in its lifetime.

The mean uncleaved egg diameter is 68 μm. While in the capsule the veligers probably feed on the albumen initially present therein. The mean diameter of the newly hatched veliger shell is 123 μm, i.e. considerably larger than the egg. Morphology of the newly hatched planktotrophic veliger is figured. Its shell has no trace of hyperstrophy, and the most conspicuous structure in the body is the pigmented mantle organ.

In larval *Epitonium,* the pigmented mantle organ has been called excretory, and in the postlarvae a purple-secreting hypobranchial gland. It cannot be both. A similar, probably homologous pigmented structure occurs in the veligers and adults of architectonicids and pyramidellids, and in the veligers of many lower opisthobranchs. The organ releases a possibly repugnatorial dye (a suspension of fine particles) when the animal is molested or dying.

The veligers grow 2.8 protoconch whorls when planktonic, during which time they may be carried considerable distances by ocean currents.

Two predators on *E. albidum* are reported: the gastropod *Thais deltoidea* (Lamarck, 1822) and the fish *Thalassoma bifasciatum* (Bloch, 1791).

Wentletraps (Gastropoda: Epitoniidae) are now well known to live with or to crawl in search for coelenterates, on which they all apparently feed. The literature on these feeding associations has been listed by Robertson (1981a). Although the literature is proliferating, little has so far been done on the ecology and life history of wentletraps. The best recent contributions are those of 1) Perron (1978) on the habitat and feeding behavior of the boreal species *Epitonium greenlandicum* (Perry, 1811), 2) Smith (1977), Salo (1977) and Breyer (1980 and unpublished) on the biology of *E. tinctum* (Carpenter, 1864) in California, 3) Robertson (1981a) on the life history of the tropical Indo-Pacific species *E. millecostatum* (Pease, 1860–1861), and 4) McDermott (1981) on the egg capsules, eggs and newly hatched veligers of the

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east North American species *E. rupicola* (Kurtz, 1860). Apart from *E. millecostatum,* none of these recently studied wentletraps extends into the tropics.

The aim of the present study was to learn as much as time afforded about the life history of *E. albidum* (Orbigny, 1842) in the tropical western Atlantic. Relatively little is known about the life histories of any tropical marine gastropods, and there possibly are significant differences between temperate species and their tropical relatives. I have already shown that *E. albidum* lives with and feeds on the actiniarian sea anemone *Stichodactyla helianthus* (Ellis, 1768) in the Bahama Islands (Robertson, 1963). The present paper shows that the same association occurs in the British Virgin Islands and Barbados. The anemone host has been known as *Stoichactis helianthus,* but Dunn (1981) has shown it to belong in *Stichodactyla.*

Zoogeography

Figure 1 shows the known geographic distributions of *E. albidum* and of *S. helianthus*. *E. albidum* extends to North Carolina, Bermuda, the southwestern Gulf of Mexico, Brazil south to Argentina, and the eastern Atlantic (Cape Verdes, Liberia, Ghana and St. Helena), all of which are places where *S. helianthus* is unknown.

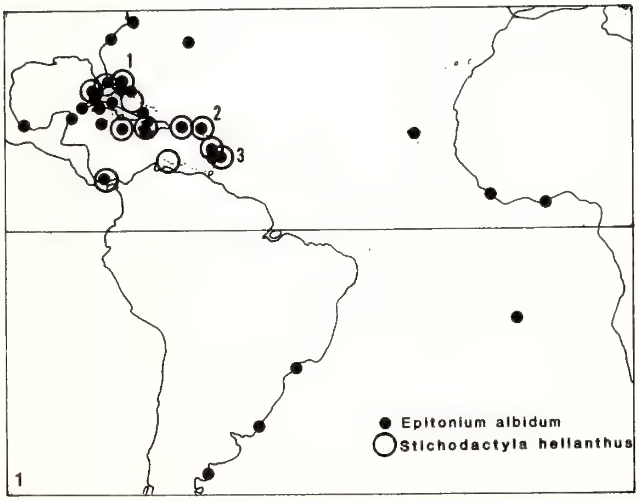

Fig. 1. The known geographic distributions of *Epitonium albidum* and of *Stichodactyla helianthus*. Locality data for the *Epitonium* are from Clench and Turner (1951) and the collections of the Academy of Natural Sciences of Philadelphia and the National Museum of Natural History, Washington, D.C. There are additional published records of *E. albidum* from Texas, Costa Rica (Caribbean coast), Surinam, and more Brazilian localities, but these are here considered doubtful or erroneous. Clench and Turner's (1951) Argentinian record is zoogeographically anomalous and may also be wrong. Locality data for the *Stichodactyla* ("*Stoichactis*") are from Pax (1910, 1924) and J. C. den Hartog (*in litt.*). A published record of Bermuda (Carlgren, 1949) is here considered erroneous. The three places where the association was studied are numbered 1 to 3.

Protandry

E. albidum is protandric and changes sex only once (Robertson, 1981b). Individuals become mature males at shell lengths between 1 and 4 mm, and become mature females at shell lengths between 7 and 8 mm. There is a long female phase which probably lasts until death.

Postlarval Growth Rate

The postlarval growth rate varies considerably, but it can be exceedingly fast (Robertson, 1983). More than one axial shell rib can be grown per day.

Scope of Study

In this paper, new data are given on *E. albidum*'s 1) abundance with its host, 2) proboscis morphology, 3) feeding, 4) spermatozeugmata and eupyrene spermatozoa, 5) egg capsules and eggs, 6) fecundity, 7) newly hatched veligers, 8) pigmented mantle organ, 9) protoconch, and 10) predators.

The following are now especially in need of study: the chemoreceptive capabilities of *E. albidum,* the role of its extrovert stylets in feeding, the duration of the planktotrophic larval stage, the morphology of the premetamorphic veliger, settlement and metamorphosis, and the postlarval lifespan.

MATERIALS AND METHODS

The old Bahamian observations were published in Robertson (1963). Research on *E. albidum* was resumed from January to March 1972 at southern Virgin Gorda, British Virgin Islands. The work was continued and completed during March and April 1980 and late January and February 1982 at the Bellairs Research Institute, St. James, western Barbados, Lesser Antilles. *E. albidum* was readily collected in all three regions.

The anemones and wentletraps are shallowly subtidal, so observations in the field and collections had to be made by skin diving. A count was kept of the number of anemones examined for wentletraps and destroyed or detached with a knife (so that the same anemone could not be examined more than once). Wentletraps found with each anemone were kept in separate snap-top vials so that not only the number of individual wentletraps could be recorded per anemone, but their sizes and sexes could be ascertained too. A record was also kept on whether masses of egg capsules were with each anemone.

Cursory observations on the morphology of the fully everted proboscis were made on animals anesthetized in 7% $MgCl_2$ mixed with sea water.

New feeding observations were made at Barbados in several large aquaria with running sea water. Each aquarium was kept stocked with one or several apparently healthy anemones attached to the side or base by their pedal discs. Between 5 and 10 wentletraps were liberated in each aquarium. The temperature was about 26° C. Whenever possible, observations were made through the aquarium glass with a 14× hand lens.

Mature, naturally shed, living spermatozeugmata with attached eupyrene spermatozoa were rarely obtained but were observed and photographed at Virgin Gorda. Eupyrene spermatozoa were observed with a compound microscope using oil immersion. They were studied unstained both in sea water and dried. Critical point drying was not possible.

In the field, egg capsules were obtained frequently in all three regions. These capsules were always sand-agglutinated. Rarely, laboratory females in sand-free petri dishes laid naked egg capsules. Capsule measurements are based on sand-covered ones, as are counts of the numbers of eggs in each capsule. These counts were made by gently splitting open each capsule and teasing the eggs out with fine needles. Eggs were measured with a calibrated ocular micrometer in a compound microscope.

Newly hatched veligers were studied at Virgin Gorda and Barbados, using the simple but effective methods taught me by the late Dr. Gunnar Thorson (apparently not previously published): pipette a swimming veliger onto a shallow depression slide, cover with a cover slip without an air bubble, and wait until the veliger becomes quiescent and yet extended (heat from the microscope light hastens the process); draw the veliger with the aid of a camera lucida, starting with the shell.

RESULTS

Habitats, Localities and Abundance

S. helianthus, the sea anemone host for *E. albidum* in the West Indies, is a fairly common shallow water species around most of the islands. According to Colin (1978), 12 m is "fairly deep for *S. helianthus* to occur." *E. albidum* was not recorded from 125 to 225 m off western Barbados in the extensive list of mainly old and empty shells published by Sander and Lalli (1982). In this study, I looked for and found living *E. albidum* with *Stichodactyla* in water no deeper than 3 m. Thus it is not known whether the feeding association occurs deeper than this. The anemone frequents both windward and leeward shores where wave action is strong to moderate. *E. albidum* was never found living away from *Stichodactyla* although the wentletrap is known from mark and recapture data (Robertson, 1983) to wander frequently from one anemone to another.

As suggested by the species name *helianthus* (sunflower), the expanded oral disc of *Stichodactyla* is broad (up to about 15 cm in diameter) and the column is short and constricted. The wentletraps usually nestle next to the base of the column under the edge of the oral disc. Only rarely are wentletraps visible before a host anemone is disturbed. *E. albidum* prefers anemones with sand around the column, and thus few wentletraps occur with anemones on near vertical surfaces where sand does not accumulate.

In the British Virgin Islands, *E. albidum* was found at southern Virgin Gorda both on the southeast (windward) coast (localities A–B) and on the southwestern (leeward) coast (localities C–D).

Locality A—Copper Mine Bay (the southern extension of Taddy [or Taylor's] Bay). *Stichodactyla helianthus* was more numerous here, although more widely dispersed, than at any of the other three Virgin Gorda localities. The anemones were in the lagoon, at the inshore side of a near-shore patch reef. They occurred in clusters on the rock substrate, dead corals and diorite boulders.

Locality B—Crook Bay. There is no offshore reef and hence the bay is continuously exposed to surf. A shallow subtidal reef flat is present, on which there are diorite boulders, rocks and dead corals. Only one *Stichodactyla* was found, but this yielded first a pair of wentletraps and eight days later a third one (hence the "2+1" in Table 1).

Locality C—Little Dix Bay. Three large anemones were clustered at the shoreward end of a large accumulation of loose rocks surrounded by a wide expanse of sand off the beach.

Locality D—Savana Bay. *Stichodactyla* was infrequent here on the shoreward part of a patch reef off the beach, all attached in several clusters to dead *Acropora palmata* (Lamarck, 1816) coral.

Combining data from all four Virgin Gorda localities (Table 1), 44 wentletraps were collected or seen. One hundred and one anemones were examined, only 26 of which were host to *Epitonium*. Numbers of wentletraps per *Stichodactyla* ranged from 1 to 5. Fourteen wentletraps occurred singly, while there were 13 occurrences of 2 or more.

At Barbados, *S. helianthus* and *E. albidum* were searched for and found only at one site on the western (leeward) coast opposite the Bellairs Research Institute just north of Holetown. The anemones are in a huge colony, the inner edge of this being approximately 40 m west of the nearest gabions on the shore. The colony is at a mean tide depth of 0.7 to 2.2 m, and covers a hummocky rock and dead coral substrate. Many of the anemones are edge to edge in an area about 9 × 2 m.

Data on the abundance of the wentletrap with its anemone host are given in Table 1. At Virgin Gorda, *E. albidum* occurs at the highest frequencies with anemones where these were most localized (i.e., localities B–D). At Barbados in 1982 as many as about 39 wentletraps were once found with a single anemone, but many fewer anemones were recorded as wentletrap hosts than in 1980. The totals for both years are comparable (63 with 100 anemones in 1980 and 65 with 80 anemones in 1982).

There sometimes were sexual pairs or aggregations, but there was no consistency about this: males also occurred with males and females with females.

Table 1. Abundance of *Epitonium albidum* with *Stichodactyla helianthus* at different localities.

Locality	No. anemones examined	No. anemones with wentletraps (and percent)	Total no. wentletraps collected or observed	No. of wentletraps per anemone									
				1	2	3	4	5	6	7	8	ca. 12[1]	ca. 39[1]
Virgin Gorda (1972)													
Loc. A	80	16 (20%)	24	11	4			1					
Loc. B	1	1 (100%)	2 + 1	1	1								
Loc. C	3	1 (33%)	4				1						
Loc. D	17	8 (47%)	14	2	6								
Barbados													
1980	100	24 (24%)	63	11	3	3	3	2		1	1		
1982	80	9 (11%)	65	3	3			1				1	1

[1] Some small specimens may have been lost and hence not counted.

Proboscis Morphology

In the genus *Epitonium* there is a long acrembolic proboscis with the true mouth at the everted tip. By contrast, *Janthina* in the related family Janthinidae has a fairly short snout from which only the tip everts (Graham, 1965). The extrovert in both genera is similar (with a ptenoglossate radula and jaws), but in some or possibly all species of *Epitonium* there is also a pair of minute stylets posterior to the fully everted jaws (the "stiletto-shaped thorns" in Robertson, 1963). According to Fretter and Graham (1962:163, fig. 101) the stylets are the termini of the ducts from one of the pairs of salivary glands. These may produce venom that is injected into the host or prey.

The fully everted proboscis of *E. albidum* is about two-thirds the length of the shell. There is a pair of stylets. Otherwise, the tip of the proboscis is like the snout of *Janthina* (see Discussion below). In *E. albidum* the skin of the proboscis is densely covered with fine immobile cilia which may play a tactile role.

Feeding

In the Bahamas, Robertson (1963) observed a small *E. albidum* feeding. Once it nipped off and swallowed a small piece of *Stichodactyla* column; another time it fed in the same manner on some *Stichodactyla* mucus.

At Barbados, feeding behavior was initiated by an *E. albidum* crawling in a zigzag path to within about a shell length from an anemone. The wentletrap would then evert its proboscis once or several times, each time probing the anemone. In response, the anemone suddenly would partially contract or writhe. Then the proboscis tip would attach and a piece of the anemone from near or at the probed area would be nipped off and swallowed. The anemone tissue then could be seen passing posteriorly inside the *Epitonium's* slowly inverting proboscis.

On eight occasions wentletraps were seen to feed on tentacles from near the edge of the anemone's oral disc. When swollen in life these tentacles are about 5 to 8 mm tall and 2 to 3 mm wide, but the walls collapse when the contained fluid is drained. Beginning at the tip, a wentletrap takes part or all of a tentacle. The smallest *Epitonium* seen to feed on a tentacle had a shell 5.7 mm long. Small proboscis size may prevent smaller wentletraps from feeding on tentacles.

On two more occasions, wentletraps 7 and 10 mm long were seen to feed on the anemone's column, each taking 3 to 5 minutes to detach a piece. Feeding on mucus was not observed at Barbados.

Monitoring was not continuous, but one fast-growing 9 to 10 mm long wentletrap fed again three days after an earlier feeding episode. Pooling all the new feeding observations, six were made during daytime and four during nighttime.

Masses of whitish mucus and orange-brown feces collect behind the operculum on the dorsal side of the rear of the foot, or are left attached to the mucous thread among the egg capsules. The feces primarily comprise clusters of cells—presumably *Stichodactyla* zooxanthellae. Neither discharged nor undischarged nematocysts were found in *E. albidum*'s feces.

No purple dye was seen to be released by the pigmented mantle organ during feeding.

Spermatozeugmata and Eupyrene Spermatozoa

Figure 2 shows the morphology of a freshly released spermatozeugma, including the longitudinally lined lamellar end (top left) and the tail with some of the eupyrene spermatozoa already detached. At Virgin Gorda, the lamellar ends were 217 ± 30 μm long ($n = 39$); the tails were 479 ± 124 μm long ($n = 34$). Thus the tail length varies considerably. The lamellar end undulates with asymmetric waves that arise proximally and the lamellar edges sometimes vibrate.

It has been suggested many times (e.g., by Graham,

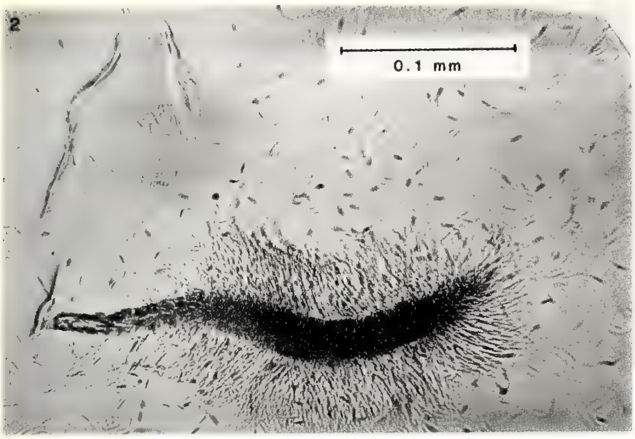

Fig. 2. Spermatozeugma (giant atypical spermatozoon) of *Epitonium albidum,* showing the lamellar end (top left) and the numerous eupyrene (functional) spermatozoa still mostly attached to the unusually short tail. Virgin Gorda.

1954) that ptenoglossan spermatozeugmata "swim" from a male to a female. Observations on living spermatozeugmata show, however, no such motility—they sink to the bottom of the container (Ankel, 1926, 1930; Wilson and Wilson, 1956; Bulnheim, 1962, 1968; present observations). I agree with Bulnheim (1962, 1968), Nishiwaki and Tochimoto (1969) and Breyer (unpublished) that an *Epitonium* spermatozeugma can pass from a juxtaposed male to a female in the ciliary water current entering the latter's mantle cavity. In aquaria and in petri dishes, a male *E. albidum* was many times seen positioned continuously for several hours or even days on the last whorl of a female (Fig. 3, but with the male closer to the female's outer lip). Thus in *E. albidum* there probably is pseudocopulation, as there definitely is in *E. tinctum* (Breyer, unpublished). The eupyrene spermatozoa must somehow make their way to the ovary.

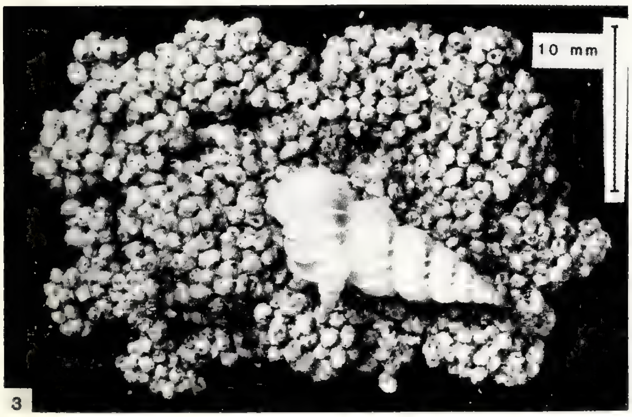

Fig. 3. Male (small) and female (large) *Epitonium albidum* together with 1,595 sand-agglutinated egg capsules found with them, possibly laid over a period of time by the one female. Simultaneously, there were many empty capsules of various sizes, early cleavage stages, trochophores, and hatching veligers. Virgin Gorda.

When more data are available on their morphology and intraspecific variation, mature spermatozeugmata (especially the lamellar ends) may prove useful in lower category epitoniid systematics.

Not all *E. albidum* eupyrene spermatozoa are attached to spermatozeugmata: white sperm balls are frequent.

Single eupyrene spermatozoa of *E. albidum* have long, slender, pointed heads about 7 to 8 μm in length, and combined middle pieces and tails about 53 to 71 μm long. The middle piece seems to have on it a spiral keel, seen only on dried out spermatozoa and not previously reported in the Ptenoglossa (Ankel, 1930; Franzén, 1955; Nishiwaki, 1964; Nishiwaki and Tochimoto, 1969). This observation requires corroboration by critical point drying and electron microscopy.

Breeding Season

Freshly laid egg capsules were found in the field at the places and on the dates given in Table 2. In the West Indies the species may breed year-round. Eggs have been found whenever they were looked for, but data are needed on October through December and for June and August.

Table 2. Localities where *Epitonium albidum* egg capsules were collected, and dates of collection.

Locality	Date
Exuma Cays, Bahamas[1]	mid May, 1966
Southern Virgin Gorda	Jan.–March, 1972
Western Barbados	March–April, 1980
Western Barbados	late Jan.–Feb., 1982
Freeport, Grand Bahama[1]	late July, 1982 (*teste* J. Worsfold)
Freeport, Grand Bahama[1]	early Sept., 1982

[1] Not one of the localities otherwise studied.

Egg Capsules and Eggs

Masses of egg capsules are commonly more conspicuous to the human eye than are the wentletraps, which often are buried in the masses or in the sand surrounding the bases of anemones. Capsules begin to be laid when individuals first become females at a shell length of about 7 mm. In the field, capsules invariably are sand-agglutinated (Figs. 3–4); this obscures their shape.

Epitonium egg capsules are all grossly similar, but in most cases there are species-specific differences in their shapes and wall thicknesses. The rare capsules laid without

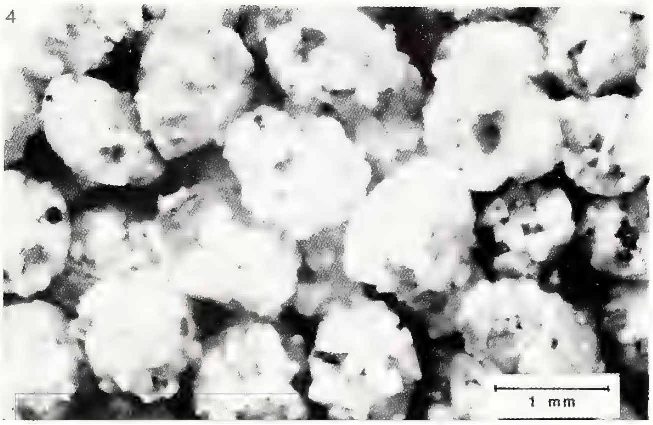

Fig. 4. Closeup of sand-agglutinated *Epitonium albidum* egg capsules. Virgin Gorda.

sand in the laboratory were ovate or elliptical in outline, with thick walls but no mucoid projections (Fig. 5); in cross section the capsules are round or elliptical. Each capsule is attached on its side to an elastic mucous thread that extends from one capsule to the next. The thread tends to bunch up, and thus the capsules are drawn into dense clusters (Figs. 3–4). One end of the thread commonly is still attached via the longitudinal groove to the pore on the under side of the foot of the female that laid the capsules. The thread definitely comes from the pedal mucous pore and not the oviducal glands.

A least at Virgin Gorda, small females lay small egg capsules containing relatively few eggs, while larger females lay larger capsules containing many more eggs (Table 3; Fig. 6). The Barbados data, necessarily based on small capsules because only small females were available, are less clearcut (Fig. 6), but capsules of the same sizes have fewer eggs in them at Barbados than at Virgin Gorda.

The diameter of the uncleaved egg is 68 ± 0.6 μm (n = 10, Virgin Gorda; the mean diameter of 10 Barbados eggs was also 68 μm). The eggs are loose inside the capsule, and

Table 3. *Epitonium albidum*: sizes of egg capsules and numbers of contained eggs laid by females of different sizes (Virgin Gorda). See Fig. 6.

Shell length of female parent (mm)	Mean capsule length (mm)	No. eggs (n = 10)
8.0	0.7	32 ± 4.4
12.6	1.1	94 ± 6.5
15.9	1.7	137 ± 9.3
not found	2.2	248 (n = 1)

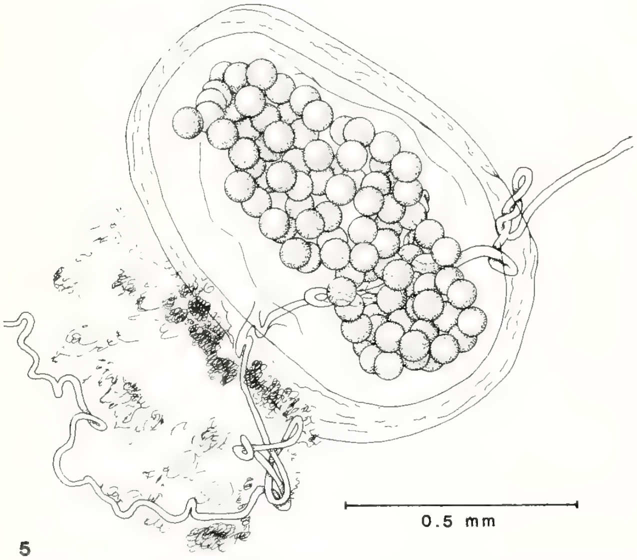

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Fig. 5. Naked *Epitonium albidum* egg capsule. Feces and flocculent mucus are adjacent to the elastic mucous thread to the lower left of the capsule. Virgin Gorda.

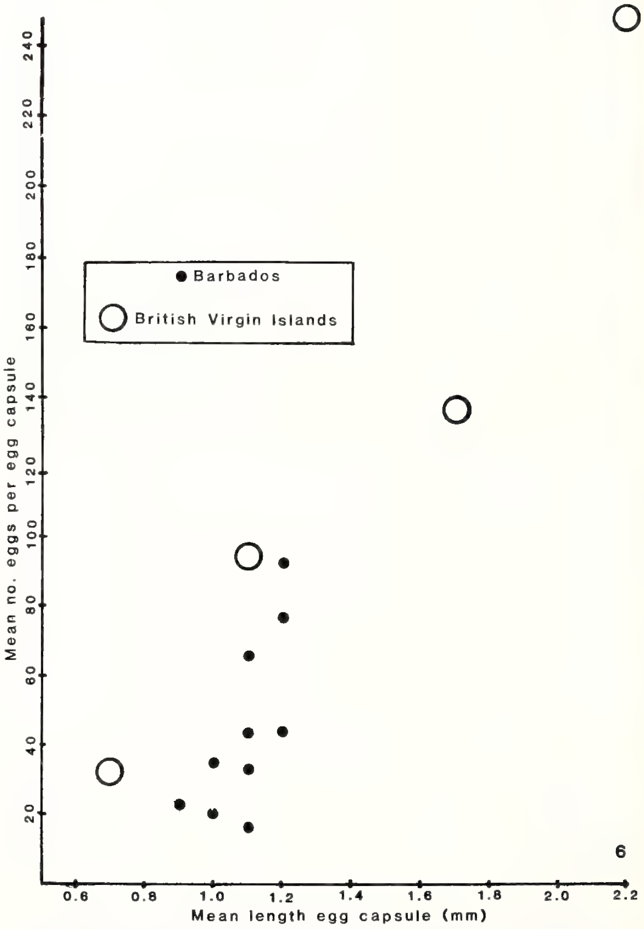


Fig. 6. *Epitonium albidum:* comparison of lengths of (sand-agglutinated) egg capsules with the numbers of their contained eggs (means of 10 counts except for the largest capsule).

they are surrounded by albumen; this disappears during development. There are no nurse eggs. At hatching, the narrower end of the capsule disintegrates and releases the veligers, leaving a thimble-shaped empty capsule. The empty capsules are durable—so much so that a large female probably retains in its mass of egg capsules all the now empty and egg-filled capsules that it ever laid. Large numbers of capsules were found only with large females (Fig. 3).

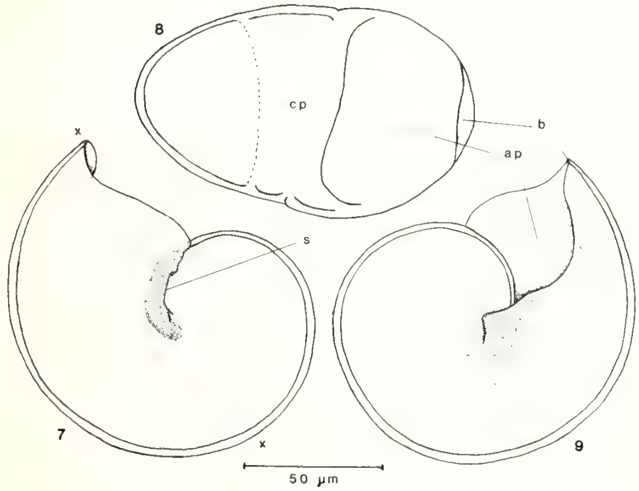
Fecundity

In the laboratory at Virgin Gorda, an *Epitonium* initially 12.6 mm long laid 331 egg capsules during 21 days (15.8/day; maximum per day: 51). In the laboratory at Barbados, an *E. albidum* 10.0 mm long laid 98 capsules overnight.

The largest number of egg capsules found in the field with a single anemone was 2,303 (Virgin Gorda). With these capsules were two females, one 15.9 mm long and the other 8.1 mm long (that must just have changed from being a male). Although it is not certain that all the eggs were produced by one individual, it is tempting to speculate that the larger animal did so—in which case it would have laid about 200,000 eggs in its lifetime. This is four times the number hazarded for *E. rupicola* by McDermott (1981).

Newly Hatched Veligers

Veligers hatched from the egg capsules 5 to 6 days after the eggs were laid in dishes at ambient temperatures (23° to 27° C.) in the laboratory.



Figs. 7–9. Right lateral (apical), apertural, and left lateral (oblique basal) views, respectively, of the shell of a newly hatched veliger of *Epitonium albidum*. Virgin Gorda. The stippling on Figs. 7 and 9 indicates where the shell is brown. Abbreviations: ap, aperture; b, beak; cp, columellar pillar; s, suture; x — x, maximum diameter.

The maximum shell diameters (Fig. 7, x — x) were 123 ± 2.3 μm (n = 10, Virgin Gorda; the corresponding Barbados mean (n = 10) was 122 μm). Thus the young veligers are considerably larger than the eggs from which they develop (mean diameter 68 μm).

The shell of the newly hatched veliger is shown in three views (Figs. 7–9). The coiling is nearly planispiral but slightly orthostrophic. The surface is smooth with faint axial growth lines. In coloration, the transparent shell is very pale yellowish green except at and near both sutures and at each end of the columellar pillar where it is brown.

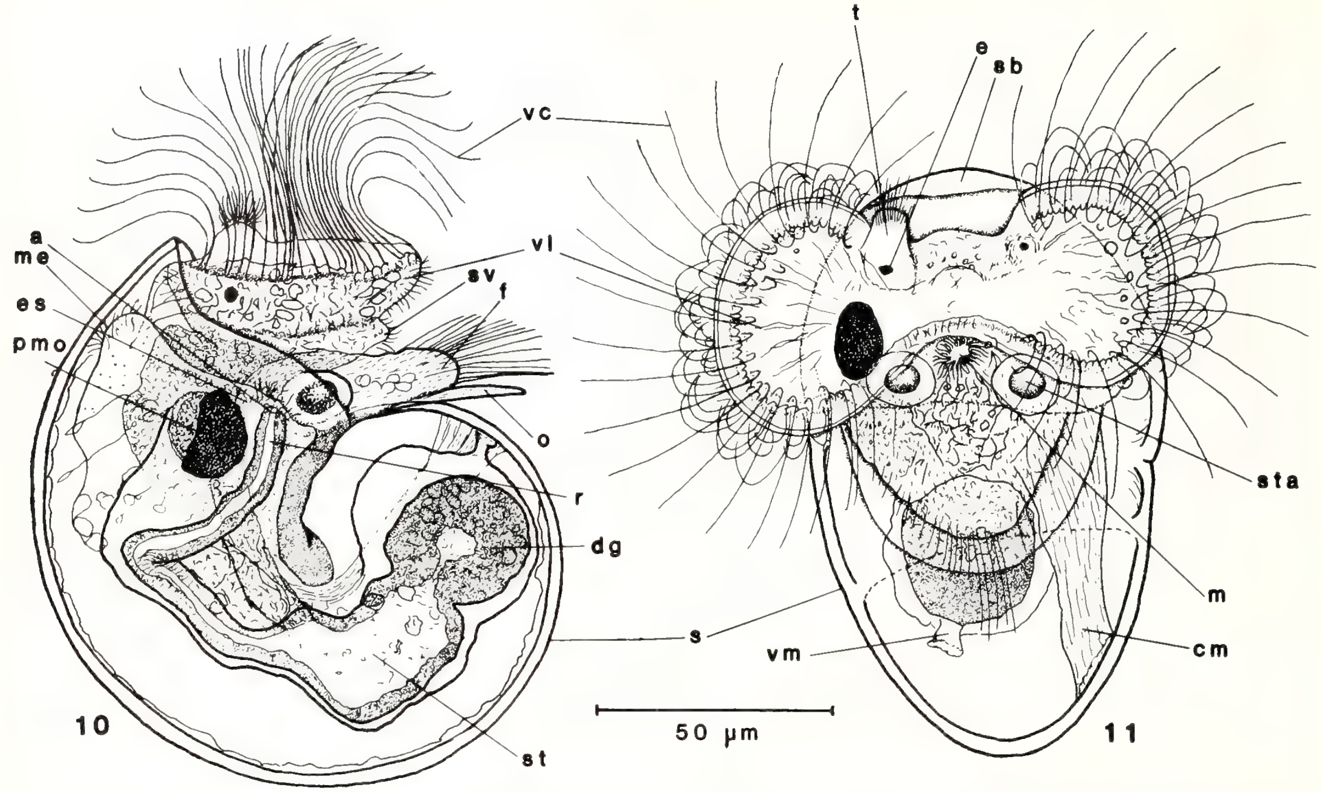
The most conspicuous structure in the veliger, and at the same time the most peculiar feature for a prosobranch, is the pigmented mantle organ (see Discussion section). The organ lies in the mantle near its edge on the right side, dorsal to the rectum and anus (Figs. 10–11). The paste-filled organ consists of a large dark brown-black portion overlain posterodorsally by a smaller dark purple portion.

Both black eyes commonly are present, but the left one may be smaller or absent at hatching. The right tentacle commonly develops before the left. An operculum is present. Cilia at the rear end of the foot are long and vibratile. The mantle edge is also ciliated, especially dorsally and near the anus. Figs. 10 and 12 show the subvelum. Except for the pigmented mantle organ and the eyes, the entire body is tinted pale yellowish green. The posterior viscera are attached inside the shell by a short length of tissue (muscle?—Fig. 11, vm). There is much variation in the sizes and relative positions of the internal organs, such as the pigmented mantle organ, stomach, digestive gland, rectum and columellar muscle.

In the absence of sufficient natural or cultured algal food it was not possible to rear the veligers. Some of them survived and were still swimming without food, and hence without growing, for about 14 days after hatching. Many of these veligers ultimately became trapped and died in the surface film of water, forming "rafts." This happens because the shiny periostracum is water-repellent (as is also the case in larval pyramidellids and opisthobranchs; other prosobranchs?).

Protoconch

The protoconch, devoid of varices and consisting of about four whorls, is commonly retained at the apex of the teleoconch (Figs. 13–14). It carries with it a record of larval life. Protoconch I, the part grown before the veliger hatches from the egg capsule, consists of about 1.2 whorls (Figs. 7–9). It is demarcated by a faint axial growth line from protoconch II, which consists of about 2.8 whorls which are slightly dorsoventrally flattened and sculptured with regularly spaced, sinuous axial growth lines which cross a subsutural spiral ridge and faint spiral lines (Fig. 15). Both these features—the shell flattening and microsculpture—are reminiscent of the *Janthina* protoconchs studied by Robertson (1971) and Richter and Thorson (1975).



Figs. 10–11. Right lateral and anteroventral views, respectively, of newly hatched *Epitonium albidum* veligers. Virgin Gorda (Barbados veligers were found to be identical). Only the right velar lobe is shown on Fig. 10. Abbreviations: a, anus; cm, columellar muscle; dg, digestive gland; e, eye; es, esophagus; f, foot; m, mouth; me, mantle edge; o, operculum; pmo, pigmented mantle organ; r, rectum; s, shell; sb, shell beak; st, stomach; sta, statocyst; sv, subvelum; t, tentacle; vc, velar cilia; vl, velar lobe; vm, visceral muscle (?)

The chief life history conclusion to be drawn from the *E. albidum* protoconch is that the hatching veliger is at a much earlier developmental stage than the settling veliger, and that the 2.8 whorls of protoconch II must be grown while the veliger is pelagic and planktotrophic. These things imply that the planktonic period is of long duration, and that the veligers may be carried by near surface ocean currents far from where they were spawned, perhaps even across the Atlantic? As in all such specialized postlarval feeding associations, it is remarkable that the presumably widely dispersed larvae are able to find the shallow water, patchily distributed host required by the postlarvae.

Predators

Two predators were observed to attack or feed on *E. albidum* at Barbados: the muricid ("thaidid") gastropod *Thais deltoidea* (Lamarck, 1822) and the bluehead wrasse *Thalassoma bifasciatum* (Bloch, 1791).

Thais deltoidea is moderately common in the crevices near and among the anemones, where it is the largest abundant predatory gastropod. On one occasion a *Thais* (shell 23 mm long and 20 mm wide) was enveloping in its foot an *Epitonium* (shell 11.0 mm long). The *Epitonium* was not drilled, but the outer lip rib and last intervarix were broken away. The two gastropods were kept together in a finger bowl for several hours. No further interaction was observed, and the *Epitonium* recovered from the attack.

Numerous small fishes, among them *Thalassoma bifasciatum,* are attracted when a *Stichodactyla* is cut up. Once a young male wrasse picked up and swallowed a small *Epitonium* before I could collect it. For a few moments, the *Epitonium* had been lying exposed on sand next to an anemone column.

DISCUSSIONS AND CONCLUSIONS

Zoogeography and Host Specificity

At least in the Bahamas, British Virgin Islands and Barbados, *E. albidum* lives with and feeds on *S. helianthus.* Considering what is presently known about the zoogeog-

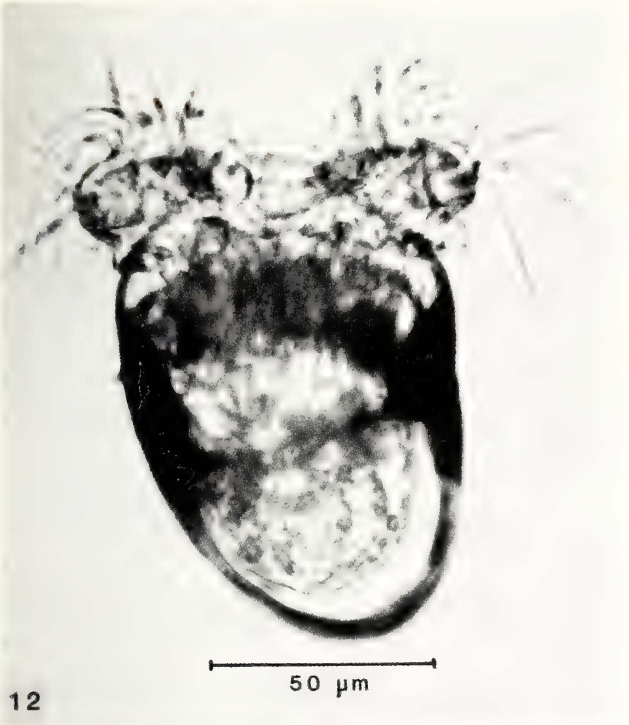


Fig. 12. Photograph of a newly hatched *Epitonium albidum* veliger (ventral view). Compare with Fig. 11 (a slightly different orientation). Virgin Gorda.

raphy of the two species (Fig. 1), it is highly desirable that comparative observations be made elsewhere. Either 1) the West Indian localities known for *S. helianthus* give a misleadingly restricted idea of its actual geographic range, or 2) *E. albidum* is not everywhere host-specific to *S. helianthus,* or 3) Clench and Turner (1951) and I have identified more than one species as *E. albidum.*

Proboscis Morphology

The snout of *Janthina,* only the tip of which everts, has been described and illustrated in exquisite detail by Graham (1965), but he and Fretter and Graham (1962:260) erred about the proboscis of *Epitonium* ("*Clathrus*"). They did not realize that this is acrembolic and that the true mouth is at the everted tip, not the base. Much of what Graham (1965) wrote about *Janthina* is applicable to *Epitonium*: there is "a pre-oral proboscis-like extrovert" at the fully extended tip, and "the two halves of the odontophore are spread apart and converted into approximately hemispherical bulges bearing the erected radular teeth." Graham (1965) was right in surmising "that all ptenoglossan radulae function in [the same] way."

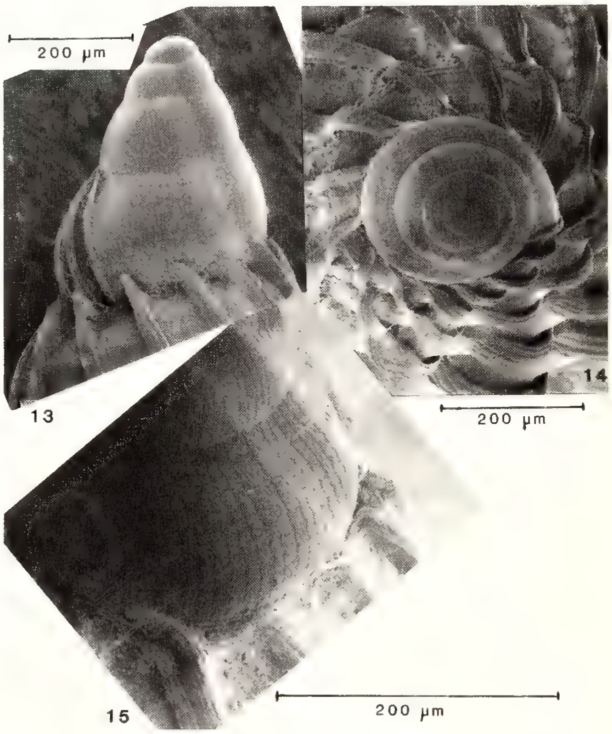
Feeding and Digestion

This study shows for the first time that *E. albidum* commonly feeds on *Stichodactyla* tentacles. It feeds on the anemone's column less commonly and on its mucus rarely. In the Indo-Pacific, *E. millecostatum* seems to feed exclusively on *Palythoa* mucus (Robertson, 1981a), but this may be an unusual diet for a wentletrap. Host zooxanthellae seem to be digested by *E. millecostatum* (Robertson, 1981a) but not by *E. albidum.* Discharged and undischarged nematocysts appear in the feces of *E. millecostatum* (Robertson, 1981a) but not *E. albidum.*

Egg Capsules, Fecundity and Veligers

The mean diameter of the uncleaved *E. albidum* egg is 68 µm. *E. millecostatum* has an almost identical mean egg diameter: 73 µm (Robertson, 1981a). Both species are planktotrophic.

E. albidum egg capsules are shown above to be laid at fast rates. *E. rupicola* was observed by McDermott (1981) to lay "54 capsules . . . within a 24-hour period." The mean number of eggs per capsule is 431 in *E. rupicola,* and thus



Figs. 13–14. *Epitonium albidum:* lateral and apical SEM views, respectively, of the protoconch and initial part of the teleoconch (with strong axial ribs). **Fig. 15.** Same, showing better the microsculpture on the protoconch. All Barbados.

this temperate species was laying eggs at an even faster rate (but for how long was the rate maintained?). *E. ulu* Pilsbry, 1921, of Hawaii, was observed by Bell (in press) to lay "a mean of 32 capsules per day, each capsule containing 500–600 eggs," another fast rate. Thus *Epitonium* not only grows fast, it is remarkably fecund as well.

The newly hatched veliger shells of *E. albidum* and *E. millecostatum* are almost identical in mean size: 122 and 124 μm (Robertson, 1981a), respectively. The veligers presumably feed on the albumen in the capsules before they hatch. In *E. rupicola,* McDermott (1981) mentions "a viscous, albuminous fluid" and Laursen (1953) states that oviparous *Janthina* embryos feed on albumen in their capsules. In *E. tinctum,* on the other hand, Breyer (unpublished) does not mention albumen and the hatching size (77 μm) approximates the egg size (70 μm).

The principal previously published descriptions and illustrations of ptenoglossan veligers are those of Haddon (1882), Fraenkel (1927), Vestergaard (1935), Habe (1943), Thorson (1946, including "*Aclis minor*"), Richter and Thorson (1975), and Robertson (1981a). Most of these reports emphasize the presence of the pigmented mantle organ (under various other names).

Larval and Postlarval Pigmented Mantle Organs

As Thorson (1957) pointed out, the pigmented mantle organ (or as he called it, the "excretory organ") of larval *Epitonium* resembles (is homologous to?) that in many larval lower opisthobranchs. Taylor (unpublished) observed the organ to be retained through metamorphosis in *Epitonium* and to become what has been called among other things the "hypobranchial gland" in the adult (Fretter and Graham, 1962:126). It seems very unlikely that the function of the organ would change from being excretory to hypobranchial at metamorphosis. Similar (homologous?) pigmented organs occur in the same position in larval and adult architectonicids and pyramidellids (Robertson, Scheltema and Adams, 1970; Robertson, 1974).

Salo (1977) determined that an anesthetic is produced in *Epitonium*'s "pallial area," but she did not make clear whether it is from the pigmented mantle organ or one of the pairs of salivary glands.

When a postlarval *Epitonium* is molested or dying, the pigmented mantle organ commonly releases dye in the form of fine purple particles in suspension. Is this dye repugnatorial? This would seem probable were in not for a fish that is reported to ingest living *Epitonium* in such numbers that its flesh becomes tinted by the dye (DuShane, 1974, 1979).

Phylogeny and Systematics

The chief finding of phylogenetic interest is that the middle piece of the eupyrene spermatozoa of *E. albidum* seems to have on it a spiral keel such as found in pyramidellids and opisthobranchs, not orthodox prosobranchs. This, if true, would be further evidence that the Epitoniidae and Pyramidellidae combine prosobranch and opisthobranch traits (Robertson, 1974).

If all pigmented mantle organs are homologous, the pattern of their taxonomic occurrence (larval and adult epitoniids, architectonicids and pyramidellids, and larval lower opisthobranchs) has bearing on the origin of opisthobranchs from mesogastropod prosobranchs.

The similarity between the protoconch microsculpture of *Epitonium* and *Janthina* spp. (first shown by Richter and Thorson, 1975) provides further evidence that the Epitoniidae and Janthinidae are closely related.

At the generic and species levels, epitoniid spermatozeugmata and egg capsules may prove useful in systematics.

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COMPARATIVE FUNCTIONAL MORPHOLOGY OF CILIA OF *CORBICULA* (BIVALVIA: CORBICULIDAE): POSSIBLE CRITERIA FOR EFFECTOR AND PUTATIVE SENSORY TYPES

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ABSTRACT

An outstanding feature of the behavior repertoire of *Corbicula fluminea* (Muller) considered here is the extreme mobility and responsiveness (especially to tactile stimuli) of the siphons. Lips of the anal siphon are notably the most responsive of the siphonal structures. Prolonged microscopic studies of serial sections of the clam's siphonal tissues revealed elaborate innervation of both siphons, but no indication of any sensory apparatus which could in turn be implicated in the distinctive behavior of the siphons. SEM studies of the epithelial surface of the anal siphon did reveal the presence of distinct, widely separated clusters of 12–20, short, upright cilia, which were seen to penetrate the "pebbled" nonmicrovillar epithelial surface. Distinctive structure of the ciliary clusters on the anal siphonal surface is especially evident when compared with SEM of other kinds of cilia in *Corbicula* (e.g. from gill, gut, mantle, gonoduct surface). These findings, along with behavioral evidence, indicate that the newly-discovered, peculiar siphonal ciliary tufts may well be the sensory organelles associated with the highly-developed tactile sensitivity of the anal siphon in *Corbicula*.

Von Uexkull (1934) characterized the *Umwelt*, the "world" relevant to an animal, as being comprised of both a sensory mode and an effector mode. With regard to the vast ciliation of many bivalved mollusks there is fairly sophisticated understanding of certain functions of effector cilia (Atkins, 1937a,b,c,; Purchon, 1956, 1978). Sensory function for ciliated or for any bivalved mollusk tissue is more difficult to establish. Accordingly, recent pertinent work on molluscan sensors is reviewed below. As is true for many non-vertebrate species (to paraphrase a comment on nematodes by Meglitsch, 1972, p. 242), we have little understanding of the sensory world bivalved mollusks inhabit. Unless the bivalve belongs to a species with well-differentiated sensors (for example, the eyes of *Pecten*), attribution of sensory function is often claimed on the basis of limited histological evidence, rarely accompanied by experimental evidence (Kraemer, 1969).

Examination of recent work on molluscan sensors reveals few investigators attempting to relate the organism's behavior to specific structures and functions of the animal. Of these, most work was done on delimited aspects of gastropod sensors. Work on chemical sense organs of opisthobranch snails has been done by Edlinger (1980). Photoreceptors of *Hermissenda crassicornis* are the subject of continuing research (e.g. Takeda, 1982). Statocysts of pulmonate gastropods have been the focus of study by Kovalev et al. (1981). Buccal mechanoreceptors in the opisthobranch, *Navanax inermis* has been subjected to neurological study by Spray et al. (1980). Kovalev (1979) has studied response of the statocysts of *Helix vulgaris*; and Zaitseva et al. (1978) have examined structure-function relationships in the statocyst of *Lymnea stagnalis*. Osphradial response in *L. stagnalis* has been the subject of a recent study by Kamardin (1976). Behavioral responses and their physiological bases are the focus of studies by Willows (1980) on *Tritonia diomeda*. Purely behavioral responses of the intertidal gastropod *Onchidium verruculatum* are examined by McFarlane (1980).

For bivalves, the recent literature is much more skimpy. Stephens (1978) studied escape responses in the queen scallop *Chlamys opercularis*. Prior et al. (1979) performed a behavioral and physiological study of "evasive" behavior in *Spisula solidissima*. Pichon et al. (1978) investigated the physiology of the sensory organ in the cruciform muscle of *Donax trunculus*. Raptorial siphonal apparatus and relation to feeding behavior and digestion in *Cardiomya planetica* is reported by Reid and Crosby (1980). Organization of certain freshwater bivalve osphradia and of statocysts was detailed by Kraemer (1978, 1981).

A continuing puzzle, much in need of investigation with modern techniques, is the fact that many bivalves respond to light although they have no "eyes" (e.g. Welsh, 1933; Bullock and Horridge, 1965; Kraemer, 1970). Some years ago Kennedy (1960) provided a clue when he was able to demonstrate that the pallial nerve of *Spisula* sp. is responsive to certain light intensities. Bivalves are also frequently sensitive to water currents and tactile stimuli (Pavlov, 1885; Wenrich, 1916; Kraemer, 1970). Still, both environmental stimuli relevant to the animals and the physical means of detection employed by bivalves for these stimuli are scarcely understood, though statocysts have been implicated (Franc, 1960).

A few characteristics of *Corbicula fluminea* (Muller), subject of the present study, may appropriately be reviewed here. In contrast to indigenous freshwater bivalves with their flared mantles open to river currents, *C. fluminea* has a thickened, fused mantle, a narrowed pedal gape, a deep siphonal pocket and two muscular, extensible, highly mobile siphons (Fig. 1) with characteristic disposition of papillae (Kraemer, 1977, 1979; Britton and Morton, 1979). While behavioral observations do not seem to implicate light as a stimulus modality for *C. fluminea,* the slightest tactile stimulus, sudden water current change or jarring of the substratum all elicit siphonal response, especially of the conspicuous, characteristically peach-colored excurrent siphon. The response may involve movement of the papillae, the distal lip of the siphon, or the entire siphon. The full response typically involves contraction and then withdrawal of the whole siphon down into the siphonal pocket.

The present study is part of a continuing effort to understand certain characteristics of the behavior of *C. fluminea* in terms of its functional morphology. Ciliary organelles recently found on the mobile, behaviorally sensitive excurrent siphon are discribed below. Aspects of the functional morphology of essentially effector cilia on gills, palps and gonopore lips are compared and contrasted with the siphonal cilia. It will be argued that size, complexity and spacing of ciliary types in *C. fluminea* may well provide clues to their effector or sensory functions. For example, converging evidence presented below from comparative histological and scanning electron microscopic studies and behavioral observations is adduced to argue for probable sensory status for the siphonal ciliary organelles.

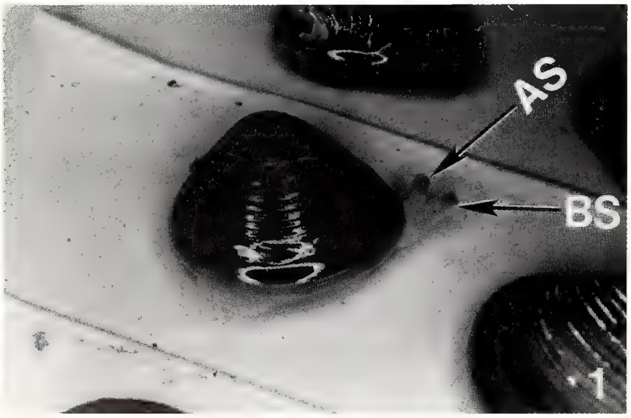

Fig. 1. Living specimen of *Corbicula fluminea* (Muller), with siphons extended. AS, excurrent siphon; BS, incurrent siphon. Horizontal field width = 12 cm.

MATERIALS AND METHODS

Histological serial sections of *C. fluminea,* made as described elsewhere (Kraemer and Lott, 1977), were used to examine ciliation and innervation of siphons, labial palps and gills and to check observations of moving cilia on living tissues, and on scanning electron micrographs. Prolonged observations were made before and during the present study on responsiveness of the siphons, especially the excurrent siphon, to tactile stimuli. Lengthy observations were similarly made on the mode of movement of several kinds of cilia on the gills and labial palps of fresh tissues with a Wild M5 stereomicroscope and with a Leitz Ortholux microscope equipped for bright-field transmitted light.

Living specimens used in this study were obtained from intake bays at Arkansas Nuclear One, near Lake Dardanelle on the Arkansas River at Russellville, Arkansas in the fall of 1981 and the spring of 1982. Subsequently the animals were relaxed in Nembutal solution. Siphonal tissues as well as tissues from gills, labial palps and gonopore region were removed, fixed in 2.0% gluteraldehyde, and then moved through cold phosphate buffer solutions and a dehydration series of ethanols. The tissues were next critical-point dried using liquid CO_2, mounted on stubs with silver adhesive solution and coated with 15 nm of gold, using a Polaron SEM Coating Unit, E 500. The samples were viewed with an ISI-60 Scanning Electron Microscope (SEM) at 30 Kv and a working distance of 15 nm.

RESULTS

Excurrent siphon epithelium

In examining the surface of the excurrent siphon with SEM, the characteristic distribution of siphonal papillae (Britton and Morton, 1979) is clearly evident (Fig. 2). One can see a few cilia on the (contracted) surface of the distal tips of a number of the papillae. A closer look at the siphonal epithelial cells' surface shows a "pebbled," probably nonmicrovillar surface (Fig. 3). In addition, at widely dispersed intervals (8–10 μm apart), discrete clusters of cilia protrude through the epithelial cell surface. Each cluster is composed of 16 to 20, curved, short (2–2.5 μm "tall") cilia (Fig. 4 a,b). These isolated ciliary clusters have a very different aspect, size and structure from all cilia examined on other epithelial cell surfaces of *C. fluminea*.

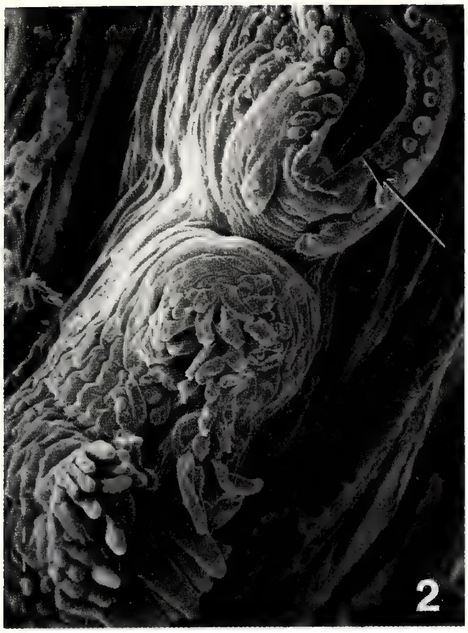

Fig. 2. Low power, SEM of the excurrent (upper) and incurrent (lower) siphons of *Corbicula fluminea* (Muller). Arrow indicates the smooth, non-papillated inner lip of the excurrent siphon, where putative sensory ciliary organelles have been found. Small slender cilia were noted on the (contracted) tips of some of the papillae of the excurrent siphon, also. Horizontal field width = 3 mm.

Labial palps

In living tissues examined for this study, the labial cilia were observed to move food particles toward the mouth in a long zig-zag. That is, particles could be followed as they were moved to the right along one ciliary row and then to the left along the succeeding ciliary row. Food particles were also observed to be moved in a direct, row-to-row course over the inner surface of the palps and into the mouth. Seen with SEM, the labial cilia were large (10–12 μm long). SEM evidence for both kinds of palp ciliary movement described above was found. Direction of movement of a particle along a ciliary row (during zig-zag movement) was clearly evident with SEM when particles were photographed lodged within ciliary rows. In such instances cilia were almost invariably seen pushed together on one side ("behind") but not on the

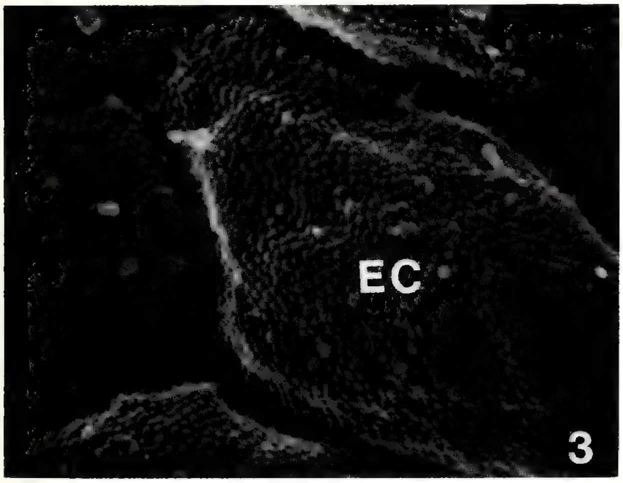

Fig. 3. SEM of distal surface of parts of several excurrent siphonal epithelial cells. EC, distal surface of an epithelial cell. Horizontal field width = 7 μm.

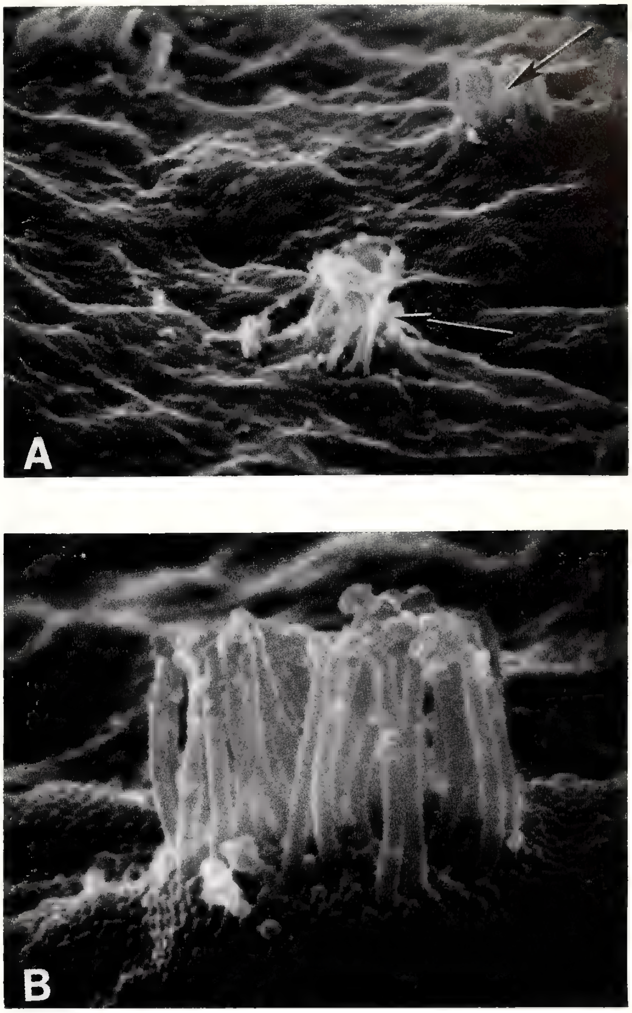

Fig. 4. SEM showing widely spaced ciliary clumps on surface of excurrent siphonal epithelium. **(A)** arrows indicate ciliary clumps. Horizontal field width = 20 μm; **(B)** a single ciliary clump protruding through the surface of an epithelial cell. Horizontal field width = 8 μm.

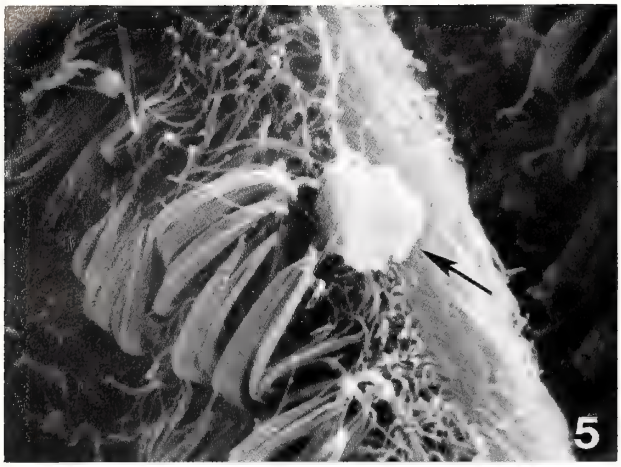

Fig. 5. SEM of labial palp cilia in *Corbicula fluminea*. Cilia are long and dense. Note crowding of cilia under particle (arrow) where effective ciliary "force" is apparently being applied. Horizontal field width = 30 μm.

other side ("in front") of the moving particle. The manner of "boosting" a food particle from one ciliary row to another is indicated in Fig. 5, where the distal tips of a group of large labial cilia may be seen tilted together "under" a food particle.

External surface of gill

With SEM, the distal edges of the gills near the food grooves were seen to display a landscape crowded with long, slender cilia (Fig. 6). Lateral surfaces of the gills, even with light microscopy, manifested certain slender cilia in addition to the large stiff cilia lining the outer edges of the water tubes (Fig. 7a). With SEM three different kinds of cilia were clearly seen organized in dense, alternating rows (Fig. 7 b,c). Most striking were the large double banks of multiple cilia (or cirri) that resemble those described by Owen and McCrae (1976) on *Nucula sulcata.* These were clearly distinguishable from the more slender, single cilia of the neighboring rows (Fig. 7 d,e). The several types of cilia on the gill surfaces were observed with light microscopy in living tissues to be associated with different kinds and directions of particle sorting and movement.

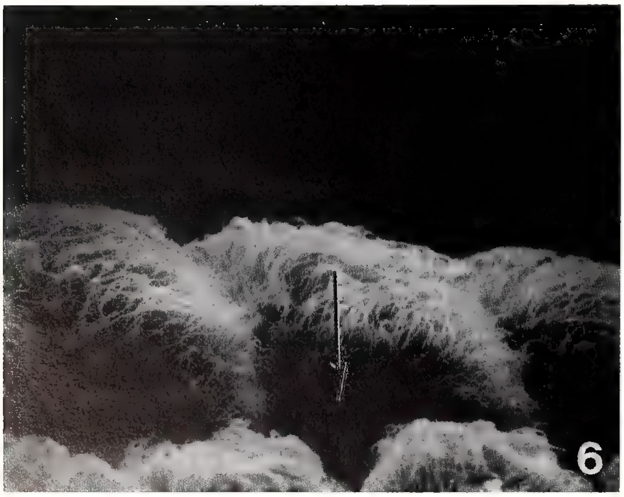

Fig. 6. SEM of ciliary surface of outer gill of *Corbicula fluminea*. Edges of several gill laminae are shown and location of food groove is indicated (arrow). Horizontal field width = 150 μm.

With SEM it appeared that: (a) the large, double-rowed, paddle-shaped, multiple cilia (cirri) with their elaborate rootlets were apparently responsible for the major movements of particles vertically along the gill lamellae; (b) the large, single-rowed multiple cilia would seem to function in selective sorting of particles; and (c) the long, slender cilia logically appeared to be those that move particles over the surface of the gill and toward currents generated by the paddle-shaped cilia.

Surface of gonoduct

While the large cilia on the surface of the gonoduct (gonopore lips) were readily seen with light microscopy, their patchy distribution was revealed only with SEM. With SEM the gonoduct surface was seen to be covered with round patches (about 10 μm in diameter) of long (10–12 μm long) cilia (Fig. 8). Functional rationale for the gonoduct surface cilia and their distinctive distribution is unclear.

Interior surface of gill

The only gill cilia found in *C. fluminea* in this study that resemble in size and shape the small cilia of the siphonal surface described above, were found at rare intervals within the cavities of the gravid inner gill (Fig. 9). These were single small cilia with unknown function. They may be associated with transport of embryos within the inner gill cavities.

SUMMARY AND DISCUSSION

With the help of SEM, it has been possible in this study to characterize several types of cilia in *C. fluminea* not previously observed. Light microscopic observations of moving cilia on living tissues of labial palps helped to establish the direction of movement of food particles over their surface; and SEM made it possible to note the manner in which groups of effector cilia provide the force to move particles. Light microscopic observations of both serial histological sections and of living tissues of gill made it evident that some cilia were larger than others, and were involved in moving particles in different ways. SEM made it possible to determine that at least three kinds of effector gill cilia are involved, respectively, in producing several specific kinds of particle movement.

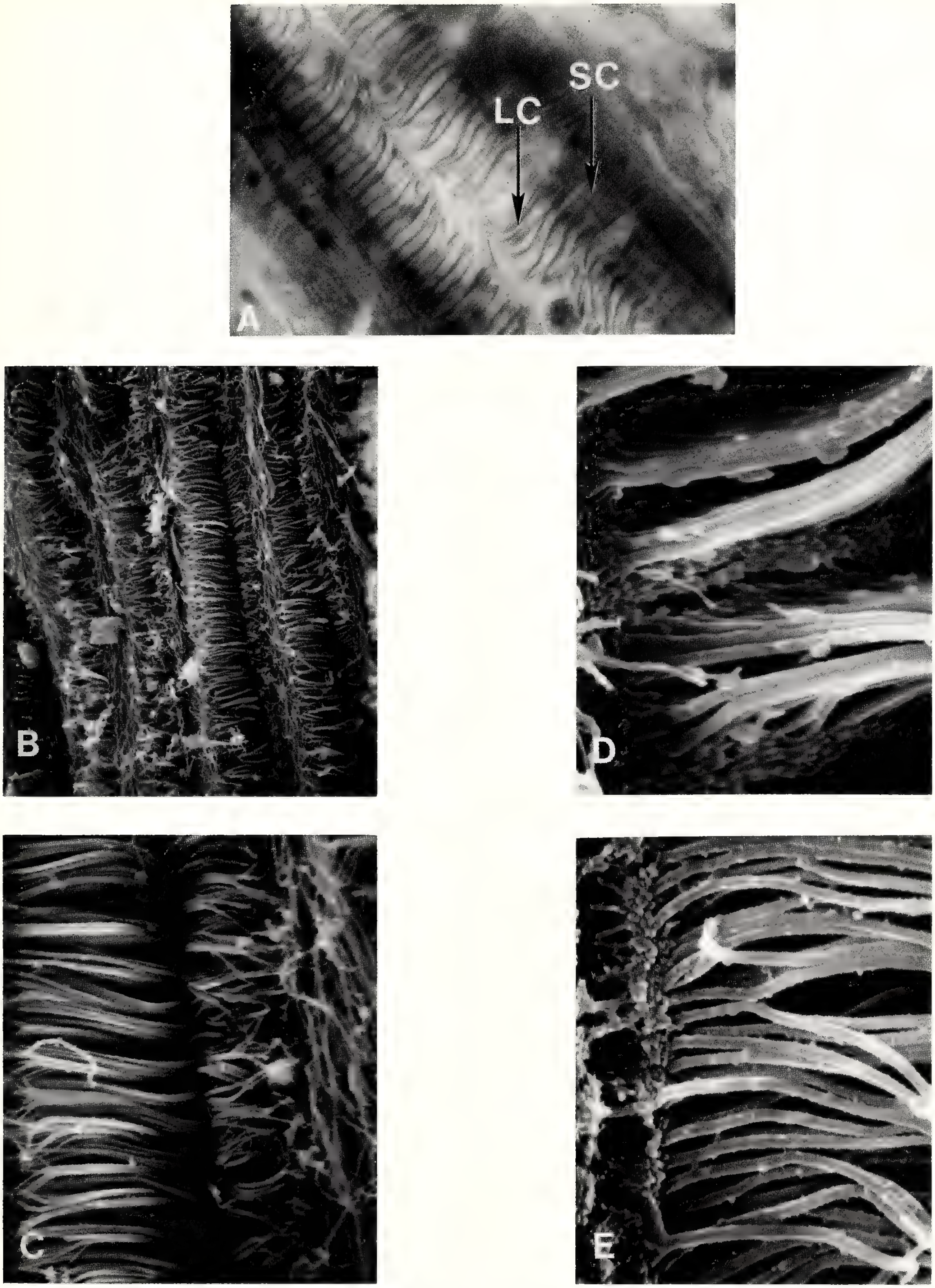

Fig. 7. Lateral gill surface ciliation of *Corbicula fluminea.* **(A)** light micrograph. LC, large cilia, SC, smaller cilia. Horizontal field width = 2 mm. **(B)** SEM showing alternating rows of three kinds of cilia. Horizontal field width = 130 μm. **(C)** Detail of B. Large double cilia are at left. Horizontal field width = 30 μm. **(D)** Large double cilia are seen to be double rows of multiple cilia (cirri). Horizontal field width = 6 μm. **(E)** Large single cilia. Horizontal field width = 7 μm.

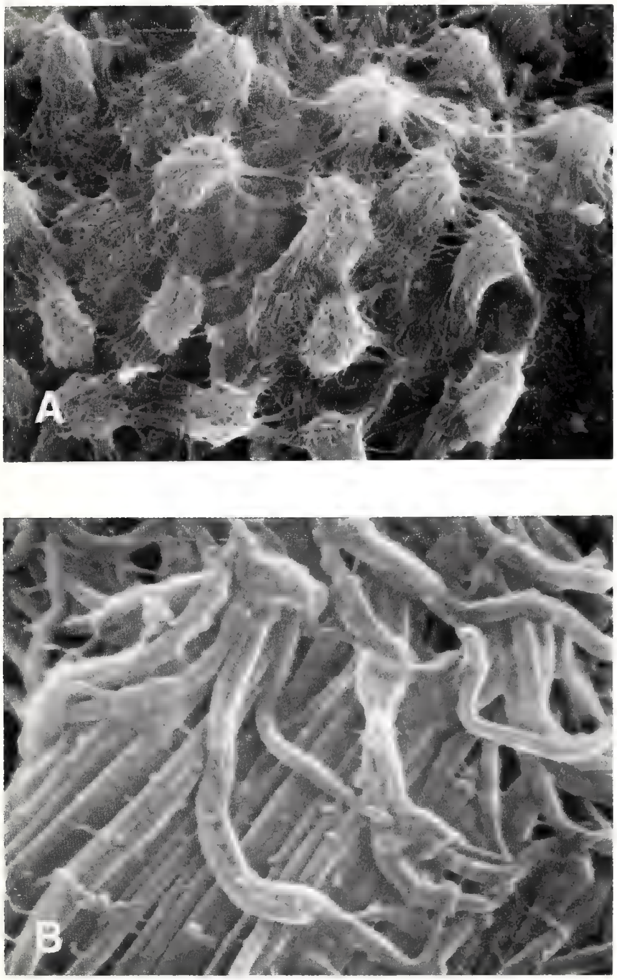

Fig. 8. Ciliation of external gonopore lip surface in *Corbicula fluminea.* **(A)** SEM of large ciliary clumps distributed over the surface of the gonopore lip. Horixontal field width 65 μm. **(B)** Detail of A. Cilia are large and interlaced with cilia from neighborning clumps. Horizontal field width = 6 μm.

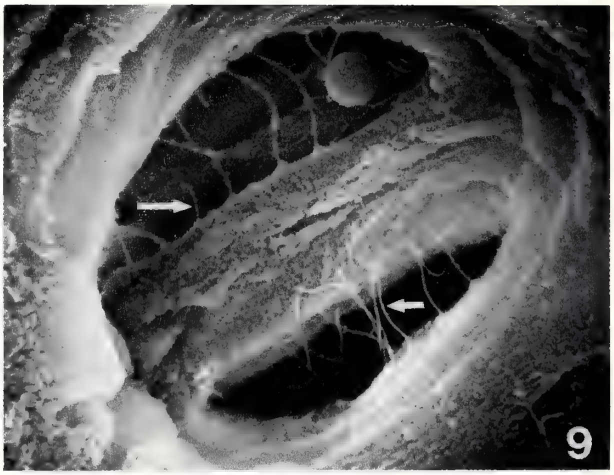

Fig. 9. SEM of interior surface of inner, gravid gill of *Corbicula fluminea.* Widely spaced, small single cilia of unknown function (arrows). Horizontal field width = 20 μm.

Light microscopic observations of gonoduct serial sections examined in connection with this study, revealed apparent groups of long cilia on the lips of the gonopore. SEM confirmed that the cilia are indeed clumped, and exhibit a patterned arrangement of patches of large, complex cilia on the epithelial surface. Function of these cilia has not been determined; but their large size, complexity and location indicate that they may function as effectors in moving ova or embryos that exit from the gonoducts.

Responsiveness of the siphons, especially the distal lip of the excurrent siphon of *C. fluminea*, to tactile stimuli was repeatedly observed throughout the study. Light microscopic studies of siphonal serial sections during this work revealed extensive innervation of siphonal musculature and the distal edges of the siphons. No histological evidence of siphonal sensory structures was found; and no conspicuous cilia were noted on the siphonal surface. With SEM in this study, an apparently "new" organelle was seen in the form of widely separated clusters of very small. curved cilia on the surface of epithelial cells of the distal lip of the responsive, excurrent siphon.

Because of their location on an exquisitely sensitive, highly innervated surface and because of their small size and distinctive appearance, it seems likely that the siphonal ciliary clumps are suitable candidates for sensory organelles. The siphonal ciliary clusters present a striking contrast when compared with cilia that have demonstrable effector functions, such as the large, complex and closely crowded cilia of the labial palps and the gill surfaces. The siphonal ciliary clumps are more nearly similar to scanty, slender cilia of unknown function found during this study in the interior of the gill cavities.

How are sensory functions for inconspicuous organelles of bivalve mollusks to be determined? One searches the literature in vain for research on bivalve sensors that in any way matches the work of Atkins (1937a,b,c), Stasek (1965), Jorgensen (1966, 1974) or Purchon (1978) on effector cilia. Using essentially morphological criteria Stasek (1966) characterized a small "ciliary sense organ" associated with the pallial eye of *Tridacna maxima,* and Kraemer (1981) did as much for the osphradial complex of two freshwater bivalves (*Lampsilis ventricosa* and *Corbicula fluminea*). Of course, physiological evidence is needed; but present day physiological techniques seem scarcely equal to the task. What alternatives are there, in the absence of physiological evidence? In the present study, the siphonal ciliary organelles described above could have been overlooked if the author had not been acutely aware of siphonal sensitivity of *C. fluminea.* The present work at least seems to indicate that persistent observation of the whole animal's behavior, and of the context and movements of living parts of the animal (e.g. cilia) may assist in evaluating functional morphology from histological and ultrastructural evidence.

From this study it may be suggested that further work on bivalve cilia may provide more evidence to indicate: (1) bivalves possess a heretofor unsuspected variety of ciliary types, each evidently suited to particular functions; (2) effector cilia types will typically be found to be large, complex and bunched in big groups, while sensory cilia will typically be found to be smaller, fewer, more isolated; and (3) cues to function of the morphological cilia types may continually be sought in careful ongoing observations of the behavior of the living organisms.

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INBREEDING AND GENETIC VARIATION IN TWO SPECIES OF *ASHMUNELLA* (GASTROPODA: PULMONATA: POLYGYRIDAE) FROM THE HUACHUCA MOUNTAINS, ARIZONA

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ABSTRACT

Electrophoretic analysis of genetic variation in eight populations of *Ashmunella levettei* and three populations of *A. varicifera* indicates that inbreeding may be a frequent occurrence in the normal out crossing method of reproduction utilized by these species. The deviations from Hardy-Weinberg expectations, a deficiency of heterozygotes, were significant at the polymorphic loci tested in both species. The $\bar{F}_{IS}$ values, the average deviation of population genotypic proportions from H-W expectations, were 0.8194 for *A. levettei* and 0.6442 for *A. varicifera*. Although polymorphic loci were detected in all populations, observed mean heterozygosity per individual was very low: 2.3% for *A. levettei*, 3.7% for *A. varicifera*. Both field studies and laboratory tests indicate that outcrossing is the usual method of reproduction for these species, thus it would appear that self-fertilization is not the cause of the observed heterozygote deficiencies.

In the last several years, the study of genetic variation in terrestrial gastropods has increased rapidly. In general, it has been found that land snails have a relatively high degree of heterozygosity per individual, and nearly all populations studied were in Hardy-Weinberg equilibrium (Selander, 1976). It is generally accepted that the latter condition indicates random mating within the population. In a few studies, the heterozygosities were very low and a deficiency of heterozygotes was detected (e.g. McCracken and Selander, 1980; Foltz et al., 1982).

An observed heterozygote deficiency can be the result of a number of factors, e.g. the Wahland effect, drift, migration, selection, and inbreeding. Sampling from what appears to be a single large panmictic population, but is actually an aggregate of subpopulations that vary in gene frequency, will produce an unexpected deficiency of heterozygotes. This is the Wahland effect (Futuyma, 1979). When a large population is subdivided, the process of random genetic drift can produce a different allelic frequency for each subpopulation. It is these different allelic frequencies that cause the Wahland effect (Hartl, 1980). Migration tends to limit how much genetic divergence can occur (ibid). Inbreeding increases the frequency of homozygotes at the expense of the heterozygotes (Futuyma, 1979). Selection in favor of the homozygote would result in a deficiency of heterozygotes leading to fixation for a single allele (Levin, 1977).

Although for many years it has been assumed that cross-fertilization is the normal mode of reproduction in hermaphroditic snails, the low heterozygosities and deficiency of heterozygotes noted above were thought to indicate that self-fertilization or a combination of self-fertilization and cross-fertilization may be a relatively frequent occurrence (Foltz et al., 1982). Self-fertilization can produce both low levels of heterozygosity and a deficiency of heterozygotes, and self-fertilization has been observed in some of the species studied.

This report will describe two species of the Polygyridae, *Ashmunella levettei* (Bland, 1880) and *Ashmunella varicifera* (Ancey, 1901), from the Huachuca Mts. of southeastern Arizona, that have both a low level of heterozygosity per individual and a large deficiency of heterozygotes. These two characteristics are apparently the result of continued close inbreeding not including self-fertilization.

METHODS AND MATERIALS

Specimens were collected from eleven localities in the Huachuca Mts., Cochise Co., Arizona (Fig. 1). In all 221

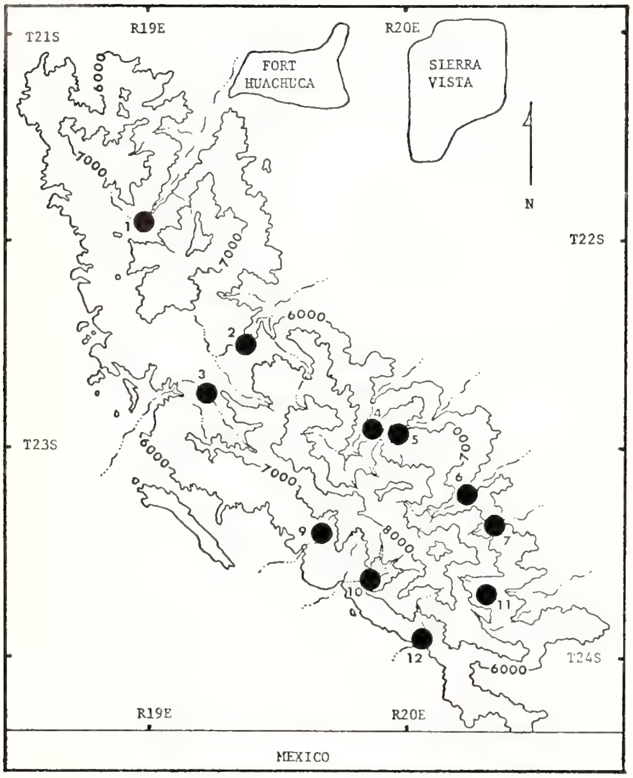

Fig. 1. Collection localities of *Ashmunella levettei* (1–7,9) and *A. varicifera* (10–12) in the Huachuca Mountains. Range and township are indicated along the borders.

specimens were utilized in the study. The areas from which the samples were collected varied considerably in size, the smallest area being approximately $10m^2$ (sites 12 and 6) and the largest area being approximately $400m^2$ (sites 3 and 11). The mean size of a collection site was approximately $200m^2$.

Horizontal starch-gel electrophoresis of a serum prepared from foot-muscle tissue as described by Brussard and McCracken (1974) and modified as indicated by Selander and Hudson (1976) was used to determine genetic variation.

Electrophoresis apparatus was as described by Utter et al. (1974), except that all tests were conducted inside a refrigerator at 4°C. Enzyme stain and buffer formulae were obtained from Siciliano and Shaw (1978) with two exceptions: a lithium hydroxide buffer (Selander et al., 1971) was used for examining glutamate oxalacetate transaminase variation, and the formula for the leucine aminopeptidase stain was obtained from Selander et al. (1971). Enzymes studied were: glucose-6-phosphate dehydrogenase, glutamate oxalacetate transaminase, α-glycerophosphate dehydrogenase, isocitrate dehydrogenase, leucine aminopeptidase, phosphoglucomutase, and tetrazolium oxidase.

Scoring of the gels followed the procedures as outlined by Woodruff (1975). The alleles segregating at a locus were assumed to be codominant.

Observed heterozygosities were determined by direct count, expected heterozygosities were calculated from the allelic frequencies. Coefficient of deviation of observed from expected numbers of heterozygotes was calculated as described by McCracken and Selander (1980). Wright's F statistics were calculated for each species (Wright 1943, 1951, 1965, 1978), and the mean genetic similarity among populations of each species was determined using Rodgers' coefficient of similarity (Rodgers, 1972).

RESULTS

Of the nine loci scored, three were polymorphic (33%), GOT, IDH, and PGM (Table 1). Of the three polymorphc loci, one (PGM-2) had three alleles segregating.

In Table 2 it can be seen that among the populations of *Ashmunella levettei* an average of 48% of the polymorphic loci have fixation for a single allele, whereas in *A. varicifera* 33% have fixation for a single allele. At the GOT-1 locus, alternate alleles are fixed in each species.

Table 3 lists the levels of polymorphism and heterozygosity for each species. There was a very low level of heterozygosity per individual and a large deficiency of heterozygotes indicated.

Table 4 summarizes the genetic properties of *Ashmunella levettei* and *A. varicifera*. The $\bar{F}_{IS}$ values, the degree

Table 1. Results of enzyme stain tests.

Enzyme		Number of loci detected	Number of loci polymorphic	Number of alleles at polymorphic locus
Glucose-6-phosphate dehydrogenase	(G-6-PD)	1	0	—
Glutamate-oxalacetate transaminase	(GOT)	2	1	2
α-Glycerophosphate dehydrogenase	(α-GPD)	1	0	—
Isocitrate dehydrogenase	(IDH)	2	1	2
Phosphoglucomutase	(PGM)	2	1	3
Tetrazolium oxidase	(TO)	1	0	—
	Totals	9	3	

Table 2. Allelic frequencies at the polymorphic loci.

	GOT-1			IDH-1			PGM-2			
Population	N	a	b	N	a	b	N	a	b	c
Ashmunella levettei										
1	20	—	1.000	18	—	1.000	20	—	.150	.850
2	19	—	1.000	18	—	1.000	20	—	.400	.600
3	23	—	1.000	13	—	1.000	23	—	.870	.130
4	20	.275	.725	12	—	1.000	20	—	.775	.225
5	20	.425	.575	14	—	1.000	20	.300	.500	.200
6	20	.150	.850	13	—	1.000	20	—	1.000	—
7	20	.250	.750	10	—	1.000	20	—	1.000	—
9	19	—	1.000	20	.250	.750	20	.150	.850	—
Totals	161	.137	.863	118	.042	.958	163	.055	.696	.249
Ashmunella varicifera										
10	20	.650	.350	20	.175	.825	20	—	.900	.100
11	20	.900	.100	19	—	1.000	20	—	.425	.575
12	20	1.000	—	20	—	1.000	19	—	.895	.105
Totals	60	.850	.150	59	.059	.941	59	—	.737	.263

of deviation from H-W equilibrium expectations, are very high, indicating a large heterozygote deficiency. F_{st} values, a measure of the heterogeneity of allelic frequencies among populations, are also high, and comparable to those of *Derocerus laeve* ($F_{st} = .194$; Foltz et al., 1982) and *Rumina decollata* ($F_{st} = .294$; Selander and Hudson, 1976). The F_{it} values, a measure of the overall degree of allelic fixation, are high, but not as high as those of *Derocerus laeve* ($F_{it} = .932$; Foltz et al., 1982) and *Rumina decollate* ($F_{it} = .827$; calculated from data in Selander and Hudson, 1976), both of which are self-fertilizing species. Rodgers' similarity index values indicate a high degree of genetic similarity among populations of each species. These values are comparable to those of other land snails, e.g. .97 among populations of

Table 3. Genetic properties of the populations studied.

		Number of loci			Heterozygosity		Coefficient of heterozygote deviation (D)
Population	N	examined	polymorphic		expected	observed	
Ashmunella levettei							
1	20	9	1		0.030	0.000	−1.000
2	19	9	1		0.056	0.023	−0.592
3	23	9	1		0.028	0.011	−0.623
4	20	9	2		0.094	0.024	−0.748
5	20	9	2		0.136	0.054	−0.594
6	20	9	1		0.031	0.024	−0.231
7	20	9	1		0.048	0.013	−0.740
9	19	9	2		0.072	0.034	−0.548
Total	161			overall	0.061	0.023	D = −0.635
Ashmunella varicifera							
10	20	9	3		0.105	0.094	−0.070
11	20	9	2		0.077	0.017	−0.850
12	20	9	1		0.021	0.000	−1.000
Total	60			overall	0.068	0.037	D = −0.640

Table 4. Genetic properties of the species studied.

	Ashmunella levettei	*Ashmunella varicifera*
Number of populations	8	3
Number of individuals	161	60
Number of loci studied	9	9
Number of loci polymorphic	3	3
Mean heterozygosity (%)	2.30	3.70
$\bar{F}_{is}$	.8194	.6442
F_{st}	.2695	.1831
F_{it}	.6780	.4693
Mean genetic identity among populations	.929	.926

Helix aspersa (Selander and Kaufman, 1975) and .94 among populations of *Arion subfuscus* (McCracken and Selander, 1980).

DISCUSSION

Analysis of the electrophoretic data for *Ashmunella levettei* and *A. varicifera* has indicated two important points concerning their genetic variability:

1. a very low level of heterozygosity per individual, 2.3% and 3.7% for these two species as compared to an average of 15% for other species of land snails (Selander, 1976).
2. an apparent overall deficiency of heterozygotes for each of the polymorphic loci, with values (Table 3) comparable to those for *Derocerus laeve* (D = −.534 to −.902) in which self-fertilization is well known (McCracken and Selander, 1980).

Drift, migration, and selection are all evolutionary forces that affect the pattern of genetic varibility (Workman and Niswander, 1970; Allard, Jain and Workman, 1968; Hartl, 1980). Chi square contingency tests (Table 5) indicate that both allelic and genotypic frequencies are significantly different from those expected on a random basis. The relatively low variation between high and low values of Chi square suggest that whatever forces are operating to cause the above pattern of genetic variation, they are operating similarly at all loci (see Workman and Niswander, 1970).

Table 5. Chi square contingency test results.

Genotypic frequencies				Allelic frequencies			
Locus	X^2	d.f.	Prob.	Locus	X^2	d.f.	Prob.
Ashmunella levettei							
IDH-1	23.949	14	$<.005$	IDH-1	26.264	14	$<.025$
GOT-1	89.940	14	$\ll.005$	GOT-1	127.260	14	$\ll.005$
PGM-2	155.980	14	$\ll.005$	PGM-2	231.778	14	$\ll.005$
Ashmunella varicifera							
IDH-1	87.677	4	$\ll.005$	IDH-1	124.678	4	$\ll.005$
GOT-1	25.760	4	$\ll.005$	GOT-1	41.920	4	$\ll.005$
PGM-2	35.482	4	$\ll.005$	PGM-2	54.823	4	$\ll.005$

The present harsh climatic conditions of southeastern Arizona restrict snails to relatively small isolated patches of favorable habitat, i.e. the shaded more moist canyons. Despite evidence that very small amounts of gene flow can prevent differentiation among populations (Hartl, 1980), it is thought by the authors that migration has had little effect on the genetic variability patterns for these particular species.

If a homozygote had a selective advantage over heterozygotes, a deficiency of heterozygotes could result. However, over time one would expect fixation for one allele or another (Levin, 1977). Differential selection among populations can cause differentiation of allelic frequencies and thus increase F_{st} values (Schaal, 1975). If one considers that among the populations in this study 52% of the polymorphic loci do not have fixation for a particular allele and the results of the Chi square contingency tests (Table 5), it would appear that selection was not the major factor causing differentiation of allelic frequencies among populations.

Random genetic drift affects the pattern of genetic variation by increasing differentiation of allelic frequencies. If neighbor populations have allelic frequencies that tend to be more alike than those of localites far apart, drift is thought to have had an affect on the differentiation of allelic frequencies (Nei and Imaizumi, 1966). Precise evaluation of the effect of drift is not possible, however the data in Table 2 tend to support some effect from drift in these variability patterns.

The Wahland effect (Wahland, 1928) is not an evolutionary force, however it can result in data that appear to show a deficiency of heterozygotes (F_{is}). That is, many subpopulations each with a different allelic frequency are grouped together to give an overall allelic frequency for the sample which then has an apparent deficiency of heterozygotes. While it is true that some of the areas sampled for this study were large and undoubtedly involved the sampling of several subpopulations, Schaal (1975) has noted that any Wahland effect in the F_{is} statistic is unlikely to be larger than the value of the F_{st} statistic. The F_{is} values are so large that a Wahland effect of the magnitude of the F_{st} values would not account for the observed heterozygote deficiency as indicated by F_{is}. In addition, two of the sampling areas were approximately 10m^2. It is unlikely in these samples that the Wahland effect was an important factor in the heterozygote deficiencies observed.

The F_{is} statistic should measure the effect of consenguineous mating within a population that has the potential to mate at random. In this case, F_{is} represents a temporary loss of heterozygosity, a loss that can be reversed by resumption of random mating (Crow and Kimura, 1970). The F_{st} statistic results from subdivision of the population. The loss of heterozygosity is attributable to permanent changes in allelic frequency (ibid).

Both *Ashmunella levettei* and *A. varicifera* are usually found in relatively small populations and they have a low vagility. One normally finds several specimens under a log or rock, suggesting a behavioral preference toward crowding. It appears that parents and offspring may remain in close proximity throughout much of their lives. All of these are factors that may cause inbreeding (Carson, 1967). Inbreeding causes a progressive loss of heterozygotes, and thus a decrease in heterozygosity per individual (Allard et al., 1968) and thus would be expected to increase F_{IS} values. Inbreeding can cause the differentiation of a randomly bred population into a series of subpopulations or inbred lines (Carson, 1967). Drift could then cause the differentiation of allelic frequencies among subpopulations. Both field observations and laboratory experiments have indicated that the only mode of reproduction in *Ashmunella levettei* and *A. varicifera* is cross-fertilization. There is no evidence of self-fertilization reported for either of these species. It would seem that some level of inbreeding not including self-fertilization is the most likely cause of the pattern of genetic variability observed in these species.

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THE DISTRIBUTION AND RELATIVE ABUNDANCE OF *LITHASIA PINGUIS* (LEA), *PLEUROBEMA PLENUM* (LEA), *VILLOSA TRABALIS* (CONRAD), AND *EPIOBLASMA SAMPSONI* (LEA)

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ABSTRACT

Field studies in 1981 showed that *Lithasia pinguis* (Lea) should not be placed on the federal List of Endangered Species because, although it is threatened in the Duck River, it is abundant in the Collins River and its tributaries. *Epioblasma sampsoni* (Lea) is apparently extinct and, regrettably, should probably be removed from that list. *Villosa trabalis* (Conrad) is properly listed as endangered. It is very rare and occurs only in the Cumberland River just below Cumberland Falls and in three tributaries of the Cumberland River in Kentucky. *Pleurobema plenum* (Lea), also endangered, has been reduced to three small populations, one in the Clinch River , another in the lower Tennessee River, and a third in the Green and Barren Rivers near their confluence in Kentucky.

The Green River, which 25 years ago may have been the richest mussel stream in North America, has been severely damaged by planned development. Mussel abundance has been reduced by about 90% and diversity by about 50%. It is urged that efforts be made to restore the middle portion of the Green River to its natural (pre-1958) condition. This can be approximated simply by stopping the practice of allowing cold, turbid water to pass through low outlets in the high dam at Green River Lake and instead by allowing only water from near the lake surface to be discharged.

During the summer and fall of 1981, ECOSEARCH, INC., carried out an investigation for the U.S. Fish and Wildlife Service to determine the present distribution and abundance of *Lithasia pinguis* (Lea, 1852) (Pleuroceridae), *Pleurobema plenum* (Lea, 1840), *Villosa trabalis* (Conrad, 1834), and *Epioblasma sampsoni* (Lea, 1861) (all Unionidae). *Lithasia pinguis* has been proposed for listing on the federal List of Endangered Species and the other species are already included on that list. The information was to be assembled from all possible sources, including field work.

A detailed report (Clarke, 1981) on the results of the work, including tabulations of the number of living and dead specimens of each species observed at each site, and ecological notes, is on file with the U.S. Fish and Wildlife Service, Twin Cities, Minnesota. The major findings, however, are given below. For obvious reasons, specific localities where endangered species still occur are not precisely defined.

RESULTS

Lithasia pinguis. Published records for this species include the type locality (Lebanon, Wilson County, Tennessee), the Duck River at Manchester, Coffee County, Tennessee (Goodrich, 1934), Caney Fork River and its branches (Goodrich, 1940; Burch, 1982), and the Duck River above Manchester, Tennessee and the Collins River below McMinnville, Tennessee (U.S. Department of the Interior, 1977). Published records from the headwaters of the Holston River and the Coosa River (U.S.D.I., *loc. cit.*) are believed to be incorrect. It is believed to be absent from Caney Fork River and it is clear that the Duck River population is endangered by Columbia Dam (Davis, 1974).

A thorough search at 16 localities in the Duck River and its tributaries near and above Manchester revealed only one sparse population of *L. pinguis*. That occurs in a short stretch of the Duck River at Manchester below Big Falls and above the mouth of the polluted Little Duck River. Streams above Manchester are either too slow-moving or too small to support *L. pinguis,* although they do contain a species of *Mudalia* (?) which resembles *L. pinguis.* A similar search of the nearby Collins River and its tributaries showed that *L. pinguis* is very abundant in the main river from above its mouth (which is backed up from the impounded Caney Fork River), throughout its free-flowing course for about 30 miles (48.3 km) upstream to a point 1.1 mi. (1.77 km) ESE of Mount Olive, Grundy Co.; in its major tributary, Big Hickory Creek, upstream for a similar distance (to 1.7 mi. (2.74 km) SSW of

Viola, Warren Co.); and in its smaller downstream tributaries (Little Hickory Creek, Barren Fork Collins River, and Hills Creek).

Pleurobema plenum. Reliable records of this rather cryptic species show that it was once widely distributed in the Ohio, Tennessee, and Green rivers and in some of their largest tributaries (Lea, 1840; Ortmann, 1919, 1926; Williams, 1969; Stansbery, 1971; and Ahlstedt, 1980).

Our survey covered 26 localities in the Green and Barren rivers in Hart, Barren, and Warren counties, Kentucky. Empty shells of *P. plenum* occured at eight sites in he Green River and at two in the Barren, but only one living specimen was found. That occurred in the Green River near Glenmore, Warren County. Shortly thereafter reliable information was received which shows that two other small living populations of *P. plenum* also exist, one in the Clinch River below Kyles Ford, Hancock Co., Tennessee and the other in the lower Tennessee River near Savannah, Hardin Co., Tennessee.

Villosa trabalis. The historical distribution of this species spanned more than 100 miles of the Cumberland River, at least from near Burkesville, Cumberland County, Kentucky upstream to Cumberland Falls, McCreary/Whitley counties, Kentucky and included several of its major tributaries from the Obey River in Tennessee to the Rockcastle River in Kentucky (Neel and Allen, 1964; Stansbery, 1971). The Cumberland River was impounded throughout this whole region in about 1950 and several of its tributaries have now been poisoned by acid mine waste or are also impounded.

Shortly after reaching the Cumberland River region I learned that the Kentucky Nature Preserves Commission (KNPC) had recently surveyed much of the area for freshwater invertebrates and that several records for *V. trabalis* were already available. I also examined the specimens on which these records were based, now at the Ohio State University Museum of Zoology, and verified the identifications. It was, therefore, decided to concentrate our efforts in those areas that had not been recently searched. Our field work covered 16 areas and resulted in the discovery of some range extensions and in confirming the presence of *V. trabalis* is Buck Creek, and Rockcastle River, and Little South Fork River. These streams, together with the Cumberland River just below Cumberland Falls (Stansbery, 1970), apparently support the only populations of *V. trabalis* that now exist.

Epioblasma sampsoni. Historically, this species occurred in the Ohio River from near Cincinnati to near the mouth of the Wabash River, in the lower Wabash River from near New Harmony, Indiana to the Ohio River, and in the White River, Indiana, presumably near its mouth at the Wabash River (information from specimen–associated data in the major museums of the U.S.). *E. sampsoni* is reported to have occurred only on bars of gravel or sand and never on mud (Sampson in Lea, 1861). Several workers, including the writer, have feared that, as in the Ohio River, impoundments and other habitat disruptions in the lower Wabash and White rivers might have caused the species to become extinct. This opinion was supported by the work of Stansbery (1970, 1971) and by two recent surveys of the mussels of the lower Wabash (Mayer, 1974; Clark, 1976) during which *E. sampsoni* was not found.

In the fall of 1981 water levels in the Wabash River remained very high and it was impossible to search that large river thoroughly. The combined experience of many local commercial mussel fishermen and dealers, located at numerous localities along the river from near its mouth to Lafayette, Indiana, was therefore utilized. A photograph of *E. sampsoni* was given to each informant and an attractive reward was offered for any information that would lead to the location of a living specimen. A month later the region was revisited and most of the informants were questioned again. On both occasions all informants declared that nothing resembling *E. sampsoni* had been seen in the Wabash River for decades. Only Mr. Virgil Carroll, an elderly mussel dealer in Mount Carmel, Illinois, remembered seeing any specimens of any species of *Epioblasma* (which he called "buzzard head"). These were taken in the lower Wabash River about 40 years ago. His experience has convinced him that they, and in addition the squaw foot (*Strophitus undalatus*) and the rabbit's foot (*Quadrula cylindrica*), are now extirpated from the river.

CONCLUSIONS

The available information indicates that although *Lithasia pinguis* in the Duck River is in jeopardy, as a species it is not endangered throughout its range and it should not be included on the federal List of Endangered Species. In addition, and most regrettably, *Epioblasma sampsoni* should be removed from that list because, as far as can be determined, it is extinct.

Villosa trabalis is very rare throughout its range and it is certainly endangered. Careful searches in the streams where it is known to occur usually reveal no living specimens, although one or two of its empty shells are occasionally found. The most productive locality, in Buck Creek, yielded only two living specimens after 2 ½ hours of searching, under excellent conditions, by two experienced collectors. It is recommended that the Rockcastle River, Buck Creek, and Little South Fork Cumberland River all be classified as Wild and Scenic Rivers and that they be protected from pollution and impoundment so that this species, and other rare species that occur there (e.g., *Pegias fabula*), will continue to survive.

The status of *Pleurobema plenum* in the Green River, and of the Green River itself, requires special attention. The Green River has been impounded by a series of six lock and dam structures from its mouth to Mammoth Cave National Park, a distance of about 200 river miles (322 km). A major tributary, the Barren River, has also been impounded from its mouth upstream to Bowling Green, a distance of 40 miles (64.4 km). In 1965 Green River Dam 4, located just below the mouth of the Barren River, was destroyed from impact with a large floating tree. This caused the water levels to decline upstream from that dam, in both the Green and Barren rivers, to the next lock and dam structure and those reaches to resume a pre-impoundment, free-flowing condition. That is the only region within the Green River System where *P. plenum* now survives.

Above Mammoth Cave National Park the Green River has also been severely altered. That is especially tragic because during the late 1950's that reach contained probably the most diverse mussel fauna—about 50 species—of any river in North America (Stansbery, 1965 and pers. comm.). In 1958 and 1959 the reach from Greensburg, Green County to Mammoth Cave was heavily impacted by oil brine pollution and whole mussel communities were killed (Williams, 1969). By 1968 many species had begun to repopulate that part of the river but in June 1969 a large dam upstream, at what is now Green River Lake, was completed. The immediate effect of that dam on the mussel fauna is unknown, but in the summer of 1981 fishermen at Munfordville, Cave City, and Park City complained that although many species of fishes previously occurred in the river, for about the past ten years fishing had been very poor and only carp, catfish, and suckers could be caught.

In July 1981 we noticed that the river at Munfordville, and above the town, was unusually cold and that a thick layer of silt covered all submerged objects. A visit to Green River Lake Dam soon revealed the reason. Cold, turbid water was being released from below the thermocline through a low outlet in the dam. Enquiries to the Corps of Engineers, the agency which operates the dam, revealed that a program was underway, in coordination with the State of Kentucky, to manage that part of the Green River as a trout stream by mantaining the temperature at 65±5°F each year from May to October.

During our survey only 24 species of mussels were found alive in the Green and Barren rivers above Green River Dam 4. Fourteen additional species occurred only as empty shells. All of these are listed below (Table 1). To facilitate comparisions with the survey by Williams (1969), the Green River divisions used by him are used here, *viz.* Area 1 includes the first riffle just inside the eastern boundary of Mammoth Cave National Park and extends upstream to Green River Lake, and Area 2 extends from below that riffle downstream to Green River Dam 4. The region below Dam 4 was not sufficiently sampled during our survey to make comparisons useful. The total numbers of living specimens which we observed were: Area 1, 249; Area 2, 53; Area B (Barren River), 40.

Species found only as occasional empty shells are (in Areas 1 and 2 only): *Pleurobema coccineum, Pleurobema pyramidatum* and *Obovaria retusa;* (in Areas 1 and B only): *Plethobasus cyphyus;* (in Area 1 only): *Quadrula metanevra, Cyprogenia irrorata, Obovaria subrotunda, Villosa lienosa, Villosa ortmanni, Lampsilis anodontoides,* and *Epioblasma triquetra;* (in Area 2 only): *Anodonta grandis.*

Table 1. Living freshwater mussels observed in the Green River system in 1981.
(Numbers of specimens expressed as % of total for each area.)

	AREA		
	1	2	B
Actinonaias carinata	71.1	7.5	0
Tritogonia verrucosa	7.2	5.7	5.0
Amblema plicata	6.8	3.8	22.5
Proptera alata	3.2	9.4	0
Ligumia recta	2.0	1.9	0
Lampsilis ovata	1.6	3.8	0
Ptychobranchus fasciolare	1.2	17.0	7.5
Cyclonaias tuberculata	1.2	0	7.5
Megalonaias gigantea	1.2	0	2.5
Fusconaia flava	0.8	1.9	0
Lampsilis r. siliquoidea	0.8	1.9	0
Elliptio dilatata	0.8	0	0
Elliptio crassidens	0.4	13.2	0
Lasmigona costata	0.4	3.8	15.0
Quadrula pustulosa	0.4	3.8	0
Truncilla truncata	0.4	1.9	0
Leptodea fragilis	0.4	0	0
Plagiola lineolata	0	9.4	2.5
Quadrula nodulata	0	3.8	17.5
Pleurobema cordatum	0	3.8	2.5
Obliquaria reflexa	0	3.8	0
Pleurobema plenum	0	1.9	0
Alasmidonta viridis	0	1.9	0
Quadrula quadrula	0	0	17.5

If a diverse and thriving mussel fauna, including *P. plenum*, is to survive in the Green River, a healthy and free-flowing riverine environment must be maintained. If Dam 4 is rebuilt, and no upstream improvements are made, all natural riverine habitats in the river below its headwaters will have been destroyed. It is recommended, therefore, that the plan to convert the middle part of the Green River to a trout stream be abandoned and that the river below Green River Lake Dam and above Mammoth Cave be allowed to return to its original condition prior to 1958. The dam has the functional flexibility to allow warm, plankton-rich water to be discharged from near its top rather than cold, turbid, and plankton-poor water to escape from near its bottom. Such a change would be of great benefit to local fishermen and to the whole aquatic biological community, including the nearly extinct species *Villosa ortmanni* (Walker, 1925), which is endemic to the Green River system.

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MOLLUSKS FROM AN ARCHAEOLOGICAL SITE IN WOODFORD COUNTY, KENTUCKY

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ABSTRACT

Over 400 mollusk shells have been deposited by Fort Ancient people (900–1650 AD) in a Woodford County, Kentucky rockshelter. The analysis of the shell remains has revealed a diverse fauna consisting of one physid and three pleurocerid snails and 20 unionid mussels. The occurrence of *Pleurobema plenum, Obovaria retusa* and *Epioblasma sampsoni* are noteworthy since these species have become increasingly rare in modern times and these collections represent Kentucky River drainage records. The species composition found indicates that during the late prehistoric period this portion of the river was a medium to large sized stream with moderate current and shoal areas. Shells were not modified as tools or adornments; however, the mollusks were apparently used as a food source. The shelter was apparently inhabited sporadically for short durations during the fall, winter and spring.

In August 1980 human skeletal remains were discovered in a rockshelter adjacent to the Kentucky River in southwestern Woodford County, Kentucky (Fig. 1). This eventually resulted in a series of preliminary excavations by the University of Kentucky Department of Anthropology in cooperation with the Kentucky Office of State Archaeology. The initial investigation yielded additional skeletal remains, various artifacts and over 400 mollusk fragments or shells from what is now referred to as the Pauzar Rockshelter (Robinson et al., 1981). This investigation has expanded the present knowledge of the Kentucky River mollusk fauna.

The rockshelter is located approximately 200 meters from the Kentucky River in a wooded area on an unnamed first order, high gradient tributary. This ephemeral stream cascades across the mouth of the rockshelter and cuts through the limestone bluffs of the palisades as it flows to the river.

A perusal of the literature indicates that the Kentucky River mollusk fauna is poorly known. The gastropods and sphaerid clams of two major Kentucky River tributaries, the Dix and Red rivers, have been surveyed by Branson and Batch (1981, 1982 respectively). Houp (1970) discussed the population dyamics of *Pleurocera acuta* in another Kentucky River tributary, Silver Creek. The mainstem unionid mussel fauna was first studied by Danglade (1922) and later by Williams (1975). Houp (1980) discussed the naiads of a portion of the Red River and Taylor (1981) surveyed the mussel fauna of Eagle Creek, another mainstem tributary.

According to Robinson et al. (1981) the Pauzar Rockshelter was sporadically occupied by Fort Ancient People from about 900 to 1650 AD. The time frame was determined by artifact correlation utilizing projectile points and ceramics, and the site's location in the Inner Blue Grass. The Fort Ancient people probably used the site as shelter during hunting expeditions and in the fall, winter and spring when food reserves were in short supply. None of the shell material found to date was modified either as adornments or as tools, thus the mollusks were apparently used as a subsistence food source.

The mollusk remains from the Pauzar shelter provided additional insight into the diversity that was once present in the Kentucky River. Two of the pleurocerids, *Pleurocera canaliculatum* and *Lithasia obovata*, were the most common constituents of the mollusk remains (Table 1). Today, the

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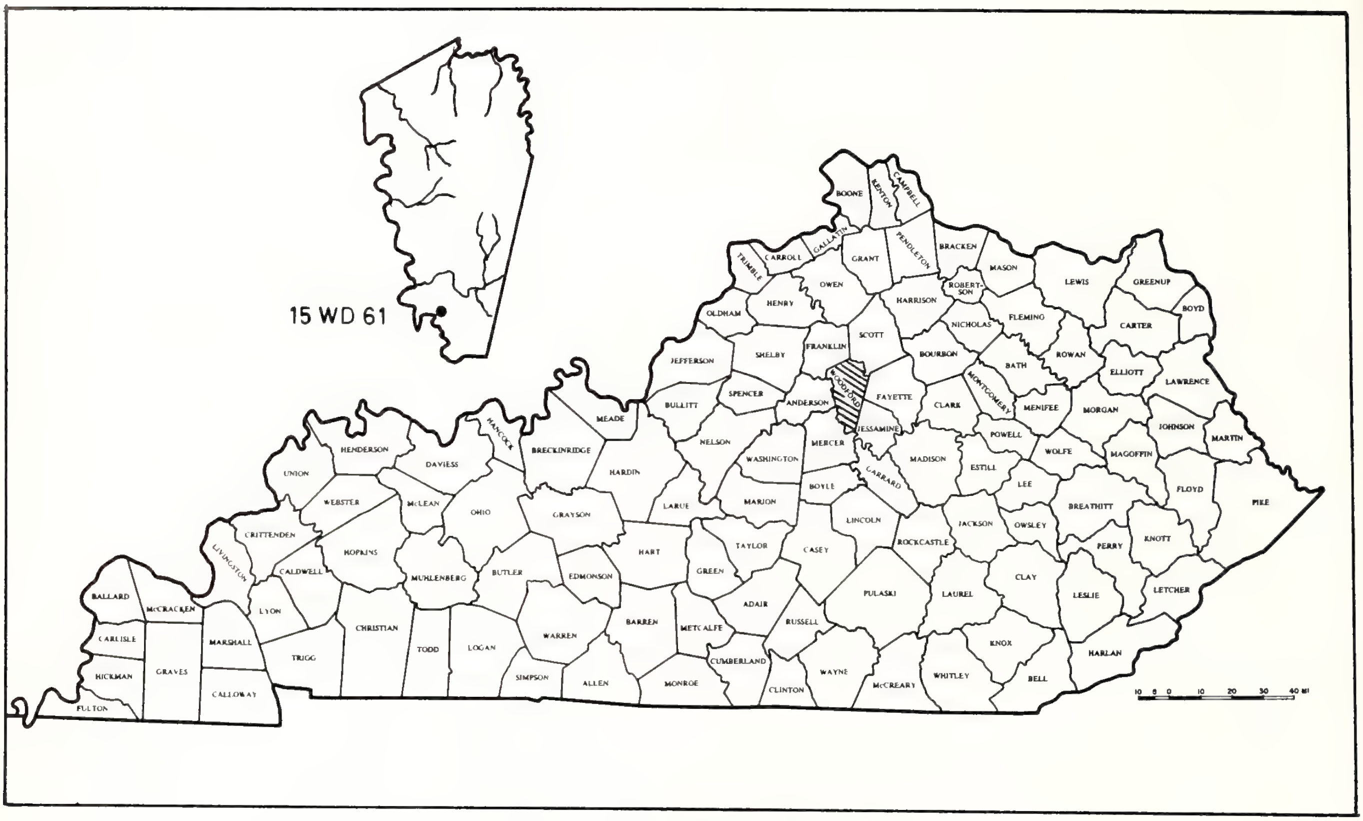
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BOONE
KENTON
CAMPBELL
CARROLL
GALLATIN
GRANT
PENDLETON
BRACKEN
MASON
TRIMBLE
OWEN
ROBERTSON
LEWIS
GREENUP
BOYD
HENRY
HARRISON
FLEMING
OLDHAM
SCOTT
NICHOLAS
CARTER
FRANKLIN
BOURBON
ROWAN
JEFFERSON
SHELBY
BATH
ELLIOTT
LAWRENCE
WOODFORD
MONTGOMERY
SPENCER
ANDERSON
FAYETTE
CLARK
MENIFEE
MORGAN
BULLITT
JESSAMINE
POWELL
JOHNSON
MARTIN
MEADE
HANCOCK
NELSON
MERCER
WOLFE
MAGOFFIN
HENDERSON
BRECKINRIDGE
WASHINGTON
MADISON
ESTILL
DAVIESS
HARDIN
BOYLE
GARRARD
LEE
FLOYD
UNION
PIKE
LARUE
MARION
BREATHITT
WEBSTER
McLEAN
GRAYSON
LINCOLN
JACKSON
OWSLEY
OHIO
CRITTENDEN
KNOTT
HOPKINS
HART
TAYLOR
CASEY
ROCKCASTLE
PERRY
LIVINGSTON
CALDWELL
MUHLENBERG
BUTLER
EDMONSON
GREEN
CLAY
LESLIE
LETCHER
BALLARD
PULASKI
LAUREL
McCRACKEN
LYON
ADAIR
CHRISTIAN
BARREN
METCALFE
RUSSELL
KNOX
CARLISLE
MARSHALL
WARREN
TODD
LOGAN
HARLAN
HICKMAN
GRAVES
TRIGG
CUMBERLAND
WAYNE
WHITLEY
BELL
SIMPSON
ALLEN
MONROE
McCREARY
CLINTON
CALLOWAY
FULTON
10 5 0 10 20 30 40 MI

Fig. 1. Location of the Pauzar Rockshelter in Kentucky.

latter is rare in the river, having been reported from the drainage previously only by Branson and Batch (1982), while *P. canaliculatum* is still common in the mainstem of the drainage. *Pleurocera canaliculatum* is found throughout the larger streams of the Ohio River system, usually occupying muddy situations (Goodrich, 1938). Collection data presented by Goodrich (1940) and Branson and Batch (1982) indicate that *L. obovata* prefers medium to large streams.

Twenty species of unionids were identified from the shell remains; of these, two species, *Elliptio dilatatus* and *Actinonaias ligamentina carinata,* exhibited the highest relative abundance of unionids. According to Parmalee (1967) both species may be found in a variety of stream sizes, in current, at depths varying from a few inches to several feet and preferring sand and gravel substrata. Seven species of particular interest, *Fusconaia maculata maculata* (=*F. subrotunda*), *Pleurobema clava, P. rubrum (=P. pyramidatum), P. plenum, Obovaria retusa, Epioblasma rangiana,* and *E. sampsoni*, exhibited low relative abundance values; this seems to indicate that they were not particularly abundant during the Late Prehistoric Period (900–1700 AD). Furthermore, all of these naiads have become increasingly rare in Kentucky and recent data (Williams, 1975; Houp, 1980; Taylor, 1981) indicate that these species are probably extirpated from the Kentucky River drainage. These seven unionids appear on the Kentucky Academy of Science–Kentucky Nature Preserves Commission's list of "Endangered, Threatened, and Rare Animals and Plants of Kentucky" (Branson et al., 1982).

This study provides the first report of *Pleurobema plenum, O. retusa* and *E. sampsoni* from the Kentucky River system. Also, *P. rubrum* has not been observed from this drainage since described by Rafinesque (1820). A review of reported habitat data (Ortmann, 1926; Parmalee, 1967; Johnson, 1978) reveals that these species are generally found in medium to large streams accompanying shoal areas.

The habitat requirements of mollusks observed at the rockshelter indicate that the Kentucky River was quite different during the Late Prehistoric Period. At that time, the Kentucky River was apparently a medium size river with a pool-riffle environment, gravel-sand substratum and moderate gradient. Today, the river is characterized for the first 2/3 of its length by a series of slow flowing, silt-laden pools that were created by the construction of 14 U.S. Army Corps of Engineers locks and dams during the late 1800's and early 1900's. Williams (1975) states that the mussel fauna of the upper portions of the Kentucky River has substantially deteriorated since Danglade's (1922) study due to perturbations of extensive coal mining operations that occur throughout the

Table 1. Mollusk remains identified from the Pauzar Rockshelter and their relative abundance.

Taxa	Relative Abundance
Physidae	
Physa sp.	< 1%
Pleuroceridae	
Goniobasis sp. (=*Elimina* sp.)	< 1%
Pleurocera canalicalatum (Say, 1821)	47%
Lithasia obovata (Say, 1829)	14%
*Unionidae	
Magnonaias nervosa (Rafinesque, 1820)	1%
Quadrula quadrula (Rafinesque, 1820)	< 1%
Quadrula pustulosa (Lea, 1831)	2%
Amblema plicata (Say, 1817)	< 1%
Fusconaia maculata maculata (Rafinesque, 1820)	1%
Fusconaia flava (Rafinesque, 1820)	< 1%
Pleurobema clava (Lamarck, 1819)	3%
Pleurobema sintoxia (Rafinesque, 1820)	1%
Pleurobema cordatum (Rafinesque, 1820)	3%
Pleurobema rubrum (Rafinesque, 1820)	< 1%
Pleurobema plenum (Lea, 1840)	< 1%
Elliptio dilatata (Rafinesque, 1820)	9%
Ptychobranchus fasciolaris (Rafinesque, 1820)	2%
Cyprogenia stegaria (Rafinesque, 1820)	< 1%
Actinonaias ligamentina carinata (Barnes, 1823)	6%
Obovaria subrotunda (Rafinesque, 1820)	2%
Obovaria retusa (Lamarck, 1819)	< 1%
Lampsilis ventricosa (Barnes, 1823)	< 1%
Epioblasma rangiana (Lea, 1839)	< 1%
Epioblasma sampsoni (Lea, 1861)	2%

*The unionid names presented here follow those listed on Ohio State University Museum of Zoology's List of the Unionid Mollusks of the Ohio River System, compiled by Dr. David H. Stansbery, May 1982.

headwaters. He also notes that only three areas in the mainstem contain extant mussel beds; however, these beds are small and recruitment is marginal at best and not sufficient to maintain the beds. No doubt this is due to habitat destruction caused by the impounding of the river by the aforementioned locks and dams, and increased siltation resulting from coal mining operations.

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SYSTEMATIC RELATIONSHIP OF THE OYSTERS *CRASSOSTREA RHIZOPHORAE* AND *C. VIRGINICA*: A COMPARATIVE ULTRASTRUCTURAL STUDY OF THE VALVES

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ABSTRACT

Crassostrea virginica occurs along the east coast of North America and northern South America, in part overlapping with, and farther south replaced by *C. rhizophorae*. While some authors recognize the two populations as separate species, others suggest that they may be the same species. We report the results of a scanning electron microscopical study of the valves of young *C. rhizophorae* from Ciénaga Grande de Santa Marta, Colombia, South America, and compared these with the ultrastructure of the valves of young *C. virginica* from Delaware, United States. Study of the periostracum, prismatic structure, foliated structure, chalky structure, myostracum, chondrophores, nymphae, ligostracum, resilium and tensilia demonstrates that at ultrastructural levels these structures are similar, if not identical, in *C. rhizophorae* and *C. virginica*, confirming the close systematic relationship of the two populations suggested by some workers.

The American oyster *Crassostrea virginica* (Gmelin) occurs along the east coast of North America from the Gulf of St. Lawrence in Canada to Key Biscayne, Florida, and in the Gulf of Mexico to Yucatan in Central America and in the West Indies (Ahmed, 1975; Galtsoff, 1964; Stenzel, 1971). In Cuba and Puerto Rico and to the south into coastal regions of Brazil, this species is replaced by the mangrove oyster, *C. rhizophorae* (Guilding) (Ahmed, 1975). Gunter (1951) gives the range of *C. virginica* as extending to Brazil, thus overlapping that of *C. rhizophorae*.

Several authors describe *Crassostrea rhizophorae* and *C. virginica* as distinct species (for example, Abbott, 1974; Galtsoff, 1964; McLean, 1941). However, Menzel (1972, 1973) reported that *C. rhizophorae* and *C. virginica* hybridize readily, and tentatively concluded (1973) that *C. rhizophorae* is a subspecies of *C. virginica*; Rodriguez–Romero et al., (1979) discovered that the morphology of the karyotypes in the two is similar; and Buroker et al., (1979) observed that *C. rhizophorae* displays a high level of genetic similarity to *C. virginica* (approximately 72%) based on an assay of electrophoretic variation in proteins. The number of chromosomes in both is similar (Menzel, 1968), but this is not uncommon as most bivalves possess 20 chromosomes in the diploid state.

The overlapping distribution of *Crassostrea virginica* and *C. rhizophorea* and the systematic affinity of the two indicated by reports of Menzel (1972, 1973), Rodriguez–Romero et al., (1979), and Buroker et al., (1979), suggest that a study of the ultramorphology of the shell of *C. rhizophorea* with reference to that of *C. virginica* should shed further information on the systematic relationship of the two taxa. The functional ultrastructure of the valves of *C. virginica* has already been described by Carriker et al., (1980) and Palmer and Carriker (1979).

In the present paper we compare the results of the study with the scanning electron microscope of the values of young *Crassostrea rhizophorae* from Ciénaga Grande de Santa Marta, Colombia, South America, (Newball and Carriker, 1983) with the ultrastructure of the valves of young *C. virginica* (Carriker et al., 1980) from Delaware, United States.

Crassostrea rhizophorae is becoming an important commercial species in tropical America and methods of culture have been studied increasingly. For example, see the papers of Wedler (1980), Jeske (1976), and Squire and Riveros (1971) for studies in Ciénaga Grande, Colombia; Martinez (1971) and Vélez (1969) in Venezuela; Bacon (1970) in Trinidad; Nikolic et al. (1976) in Cuba; and Nascimento et al. (1980 a,b) in Brazil. As Ahmed (1975) in Cuba; and Nascimento et al., (1980 a,b) in Brazil. As Ahmed (1975) points out, knowing the precise taxonomic identity of a species is important, not only commercially, but also academically. Our study contributes further information on the close systematic position of *C. rhizophorae* and *C. virginica*.

MATERIALS AND METHODS

Oysters

Specimens of *Crassostrea rhizophorae* were obtained from an experimental planting of oysters established by INVEMAR (Instituto de Investigaciones Marinas de Punta de Betin) in the lower more saline part of the estuary, Ciénaga Grande de Santa Marta, Colombia (Squire and Riveros, 1971; Jeske, 1976; Wedler, 1980). Oysters had set on sheets of plastic held in cages, and ranged in height from approximately 1 to 3 cm. They were transported alive by air to the College of Marine Studies, Lewes, Delaware, where they were maintained in segregated aerated aquaria on a mixture of algae (*Thalassiosira pseudonana* 3H Hasle et Heimdal and *Isochrysis galbana* Parke) raised in the maricultural facility of the College.

During the five months (September 1981 to January 1982) that oysters were thus maintained about half of the population lived and individuals added several millimeters of new shell. Deaths that occurred, primarily in early September, were attributed to the fact that oysters prior to collection in the field had suffered from prolonged exposure to low salinities resulting from excessive rainfall and weaker oysters were unable to survive transportation. Height of the shell of oysters whose valves were employed in the ultrastructural examination ranged from 1.2 to 2.3 cm. Valves of only live growing oysters were taken for the study of valve surfaces.

Preparation for Electron Microscopy

Opening of oysters, cutting of valves, cleaning of surfaces with Clorox (5% of full strength for 1 min), detachment of the adductor muscle from valves, dissolution of the ligament for exposure of chondrophores and nymphae (prolonged treatment with Clorox), and controlled fracturing of specific parts of valves followed procedures described in detail by Carriker et al. (1980) and Newball and Carriker (1983).

Shell specimens were dehydrated by immersion in several changes of absolute ethyl alcohol, critical-point dried, and mounted on scanning electron microscope aluminum pin stubs with silver paint. Mounted specimens were held in an oven at 70°C or in a vacuum desiccator until time for coating and examination in the scanning electron microscope (SEM). Coating was done in vacuum, first with a layer of carbon and one of gold (400–600 A) in a directional evaporator, and secondly in a sputter coater just prior to placement in a Philips PSEM 501. Scanning analyses were conducted during the period October-December 1981 at magnifications ranging from 20 to 2,500X and at accelerating voltages between 15 and 30 Kv.

Ultrastructural Analyses

Scanning electron micrographs were taken of the range of variation of shell surfaces, layers, microstructures and their transitional zones. Each ultrastructure was analyzed in at least three different oyster shells. Unetched natural shell surfaces and fracture sections proved the most informative.

Micrographs were classified in the following categories: periostracum, prismatic structure, foliated structure, chalky structure, myostracum, chondrophores, nymphae, ligostracum, resilium, and tensilia. Dimensions of microstructures and layers varied in different regions of the same individual oyster valves and in those of different individuals. In the representative micrographs accompanying this text the actual horizontal width of each micrograph is given for ease of comparison. Terms used for ultrastructures are those defined by Carriker et al., (1980) and by Newball and Carriker (1983). A review of the literature on the ultrastructure of oysters is presented by Carriker et al. (1980).

RESULTS

Comparison of Fine Structure of Valves of *Crassostrea rhizophorae* and *C. virginica*

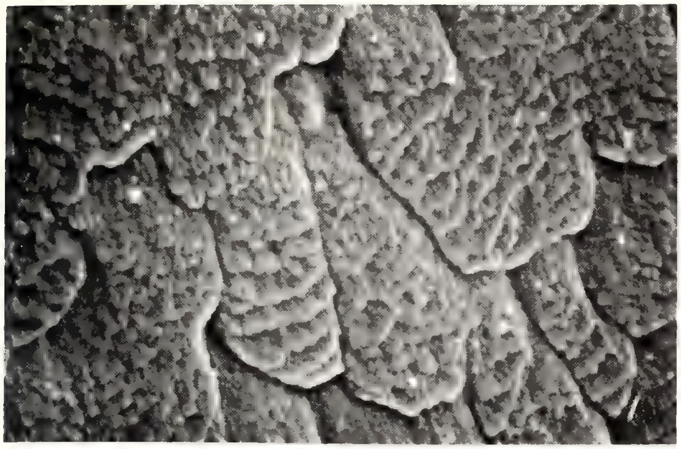
The ultramorphology of the valves of *Crassostrea rhizophorae* has been described by Newball and Carriker (1983). In this section we compare the ultrastructure of the valves of *C. rhizophorae* with that of the valves of *C. virginica* (Carriker et al., 1980), and illustrate aspects of the fine structure of *C. rhizophorae* (Figs. 1–19) that further elucidate the ultrastructure of the valves of both *C. rhizophorae* and *C. virginica*.

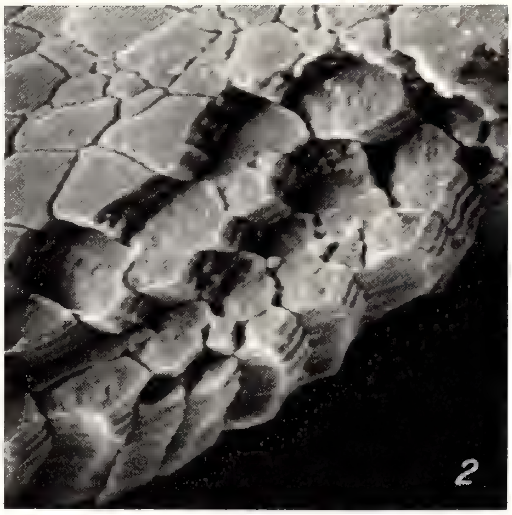
Periostracum

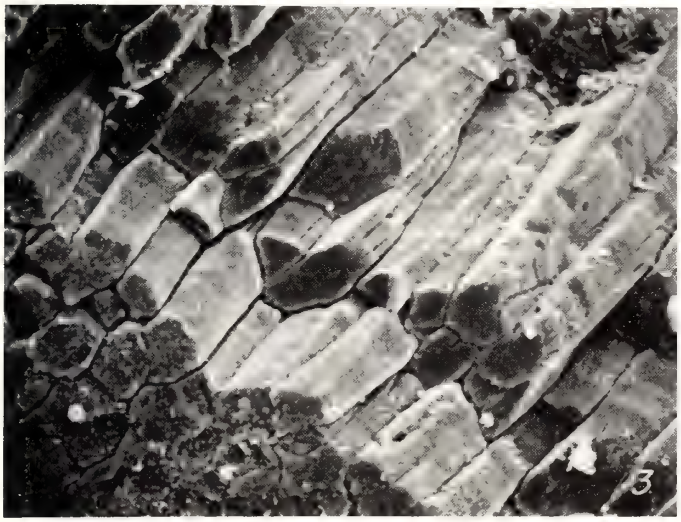
The newly formed periostracum of both right and left valves of *C. rhizophorae* is an extremely thin single layer and closely resembles that of *C. virginica* even to the pattern of folding and wrinkling especially where shell growth has been interrupted.

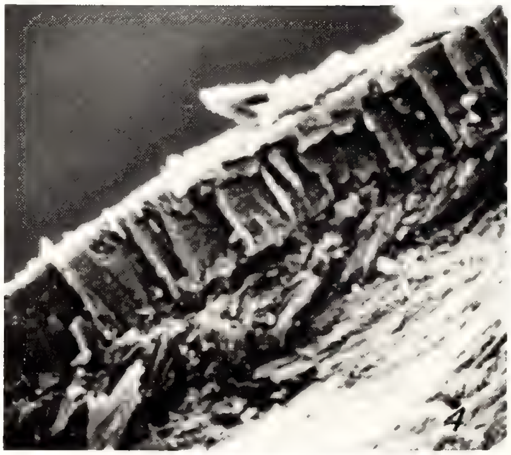
Prismatic Structure

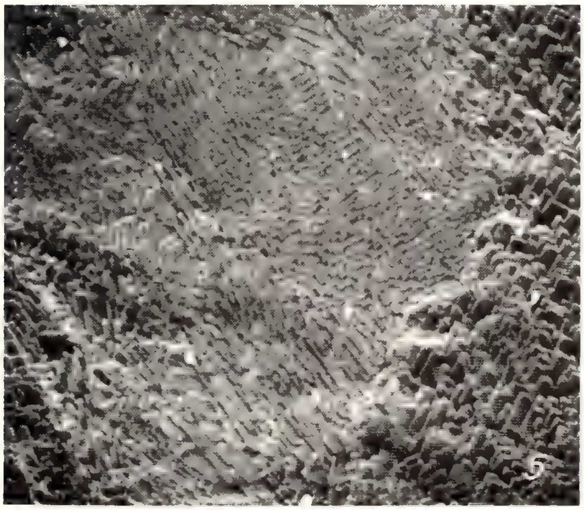
Examination of exterior, interior, and fracture surface of the right and left valves of *C. rhizophorae* disclosed an











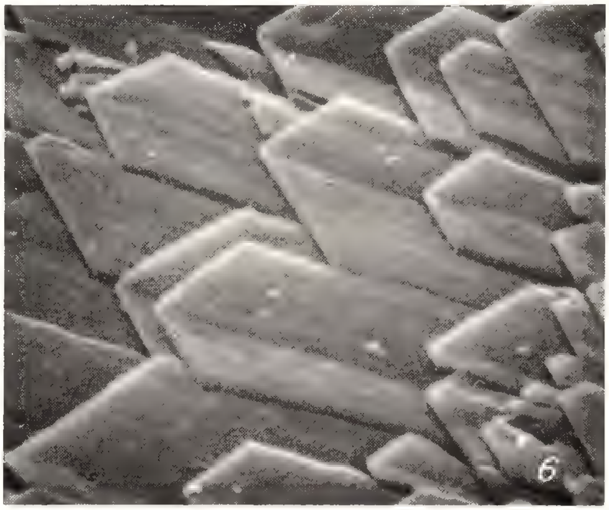


Fig. 1. Mantle-facing surface of prisms (large units) overlain by newly forming foliated laths (small shingle-like units) at ventral margin of right valve. Horizontal field width = 80 μm. **Fig. 2.** Fracture of prisms in right valve, mantle-facing view. Strata in prisms and interprismatic spaces exposed by treatment with Clorox. Horizontal field width = 115 μm. **Fig. 3.** Fracture of prisms in right valve, mantle-facing view. Strata in prisms and interprismatic spaces exposed by treatment with Clorox. Horizontal field with = 155 μm. **Fig. 4.** Fracture of thin prismatic layer of left valve, overlying foliated structure. Horizontal field width = 60 μm. **Fig. 5.** Mantle-facing surface of foliated structure of right valve at umbonal region. Horizontal field width = 70 μm. **Fig. 6.** Mantle-facing surface of foliated structure of right valve ventral to adductor muscle. Horizontal field width = 20 μm.

ultramorphology closely similar to that of *C. virginica*. For example, the unusual overlapping, tongue-like prisms in the right valve of *C. virginica,* less common than the typical columnar, closely packed prisms, are also present in *C. rhizophorae,* and resemble those in *C. virginica* where foliated laths had begun to form on surfaces of prisms (Fig. 1). The polygonal design on interior mantle-facing prismatic surfaces (Fig. 2), as well as in stratified sectional views of these prisms (Fig. 3), so characteristic of this structure in *C. virginica,* is also common in *C. rhizophorae*.

As in *Crassostrea virginica* the single stratum of prismatic shell on the left valve of *C. rhizophorae* is extremely thin (Fig. 4), a feature that prompted earlier workers to conclude that this layer was absent in *C. virginica* (Carriker et al., 1980).

The organic matrix that binds together the mineral cores of prisms is typically conspicuous in prismatic shell of both *Crassostrea virginica* and *C. rhizophorae.*

Foliated Structure

Study of mantle-facing and fracture surfaces of the foliated shell of right and left valves of *Crassostrea rhizophorae* revealed an ultrastructure closely similar to that of *C. virginica.* As in *C. virginica* the inner and most massive part of each valve of *C. rhizophorae* consists of tightly packed, long, slender laths (Fig. 7). Characteristically, orientation of laths at the mantle-facing surface between the adductor muscle and the umbone is generally varied (Fig. 5,8), whereas that of laths lying between the adductor muscle and the ventral edge of the valves is generally uniform (Fig. 6,7), a feature strongly reminiscent of that in *C. virginica.* The prominent longitudinal groove on the exposed surface of many laths in both *C. rhizophorae* and *C. virginica,* especially in the region ventral to the adductor muscle, is clearly illustrated in Figure 6.

Chalky Structure

Mantle-facing and fracture surfaces of islands of relatively soft, porous, chalky white shell that occur randomly in the valves, reveal a similar ultramorphology in *Crassostrea rhizophorae* and *C. virginica.* The surface of chalky structure lying against the mantle epithelium is spongy in appearance (Fig. 9). In fracture sections the parallel arrangement of blades and lateral leaflets is clearly visible (Fig. 10), giving an overall characteristic honeycomb appearance.

Myostracum

The single adductor muscle scar on each valve is similar in *Crassostrea rhizophorae* and *C. virginica,* displaying characteristic lines of growth as the scar increases in size and migrates ventrally (Fig. 11). A feature not often seen in *C. virginica,* but common in specimens of *C. rhizophorae* that we examined is a relatively prominent elevation of foliated structure covering the dorsal boundary of the scar. Ventral to the scar there lies a zone of characteristically granular transitional material that overlaps the foliated laths (Fig. 12) and is deposited prior to the ventral movement of the adductor muscle as the bivalve increases in size.

Hinge Ligament

As in the case of *Crassostrea virginica,* the ligament consists of a relatively thin band of elastic organic material hidden from outside view within the opening-closing pivotal axis of the valves at the umbonal region (Fig. 13). The ligament consists of a central resilium (supported between chondrophores of the two opposing valves) and an anterior and a posterior tensilium (housed between nymphae of opposing valves) (Fig. 14). Organic matter of the resilium is reinforced with long fine mineralized fibers dorsoventrally oriented within the ligament. These fibers become visible when the organic matter of the resilium is dissolved with Clorox (Figs. 15, 16). Interruption in growth by layering of resilial fibers is indicated in Fig. 15. Tensilia lack fibers and consist only of a homogeneous organic material.

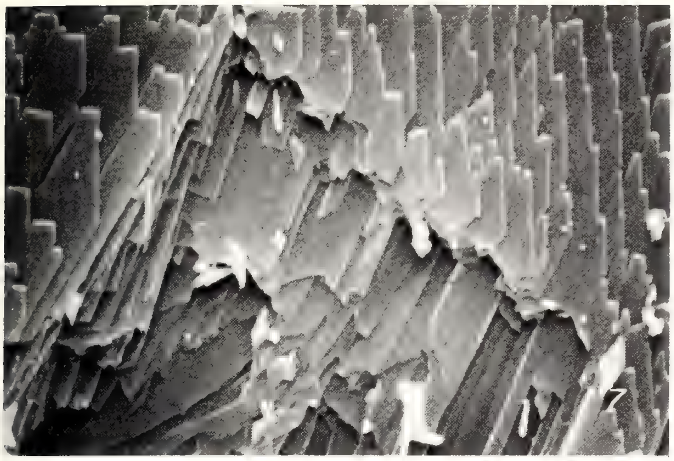
Hinge Chondrophores and Nymphae

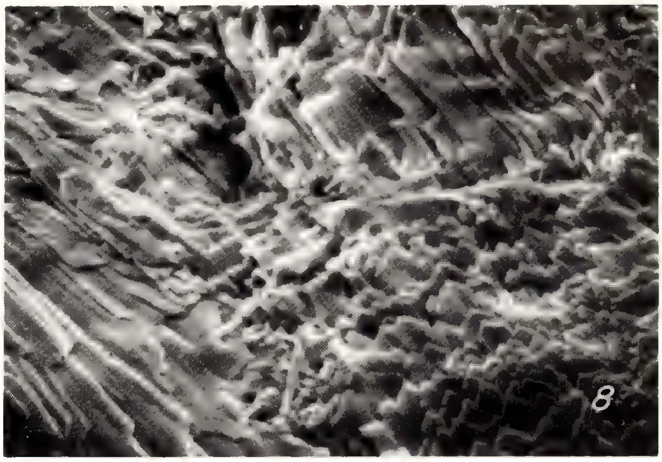
Dissolution of the ligament (resilium and tensilia) with Clorox exposes the surface of the mineralized shell to which it is affixed (chondrophores and nymphae) (Fig. 17). A thin mineralized layer, the ligostracum, binds foliated structure of the shell in the umbonal region to the organic ligament. The ligostracal prisms of the chrondrophore are strongly annulated (Fig. 18), whereas those of nymphae tend to be oriented at right angles to the surface of the underlying foliated structure (Fig. 19). The ultramorphology of the hinge structures in *Crassostrea rhizophorae* and *C. virginica* is identical.

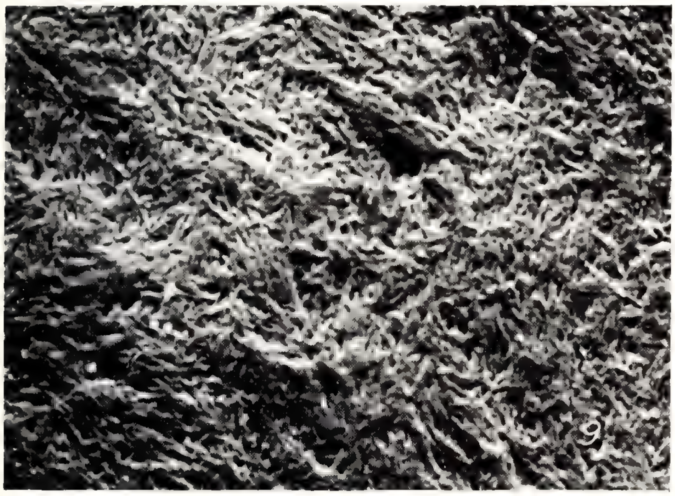
DISCUSSION AND CONCLUSIONS

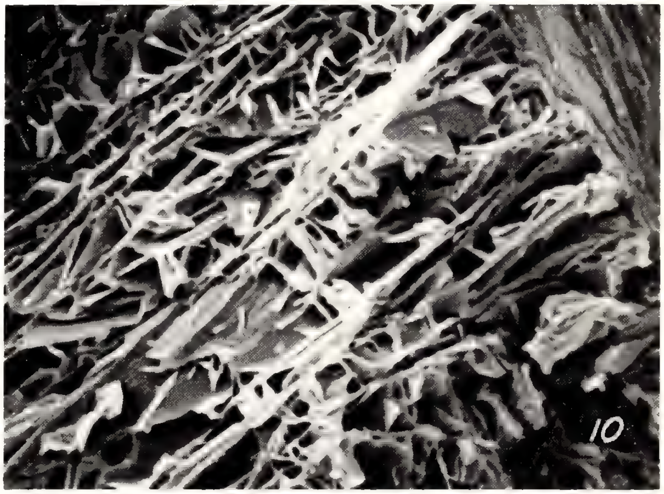
Populations of *Crassostrea virginica* cover the broad range of some 5,000 miles (8,045 km) north and south on the east coast of America, extending from cold temperate through subtropical to tropical habitats. Although the species exists as several physiological races (Stauber, 1950), differences seem to be only at the gene level, and all races are apparently structurally similar, no morphological divergence having occurred according to Ahmed (1975). Stauber (1950) postulated that *C. virginica* formerly had a discontinuous distribution, reproductive isolation resulting from differences in critical spawning temperatures. Man, however, by obliterating the discontinuous distribution of the species, has interrupted the process of speciation.

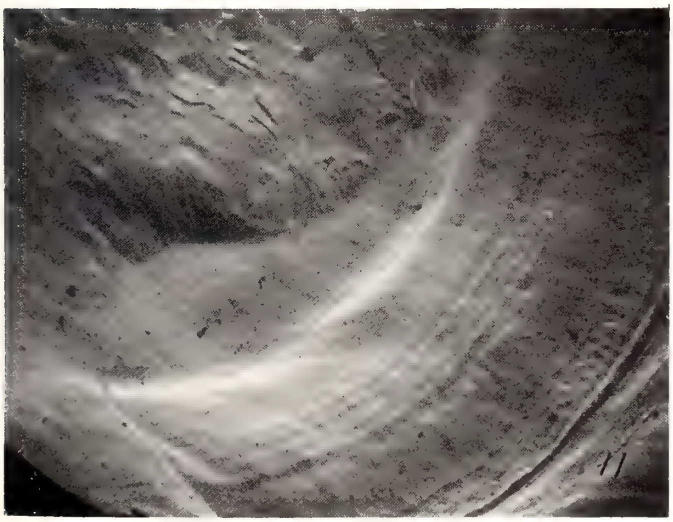
At the peripheral southern end of its range, it appears that *Crassostrae virginica* has diverged morphologically resulting in three *C. virginica*-like "species": *C. rhizophorae* widely distributed in Central and Northern South America and the Caribbean Islands, and *C. guyenensis* and *C. lacerata* in











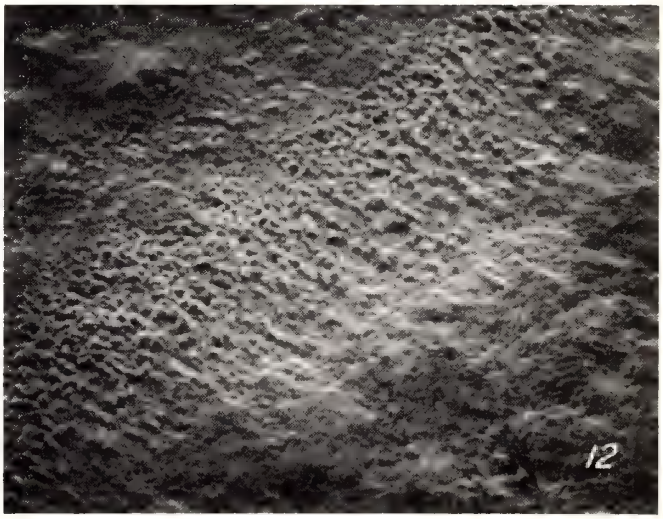
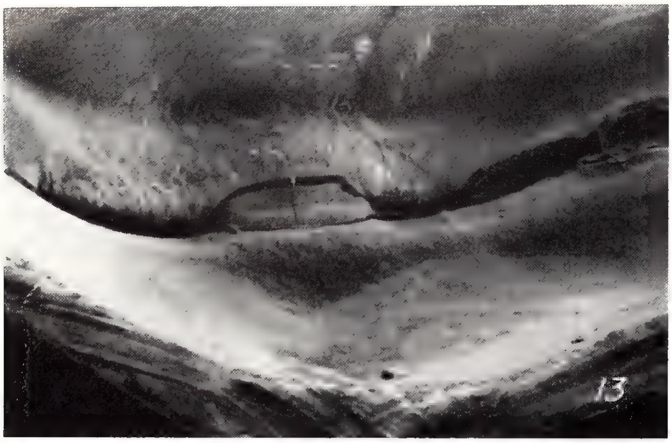
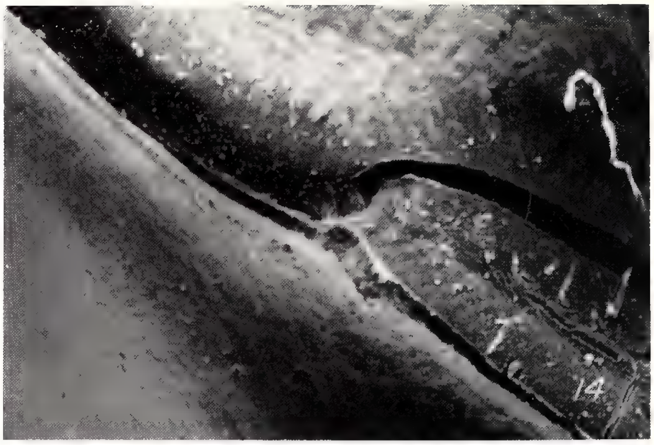
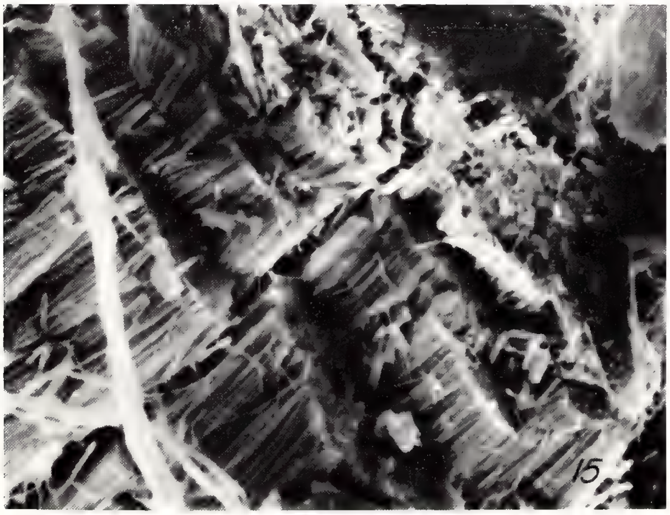
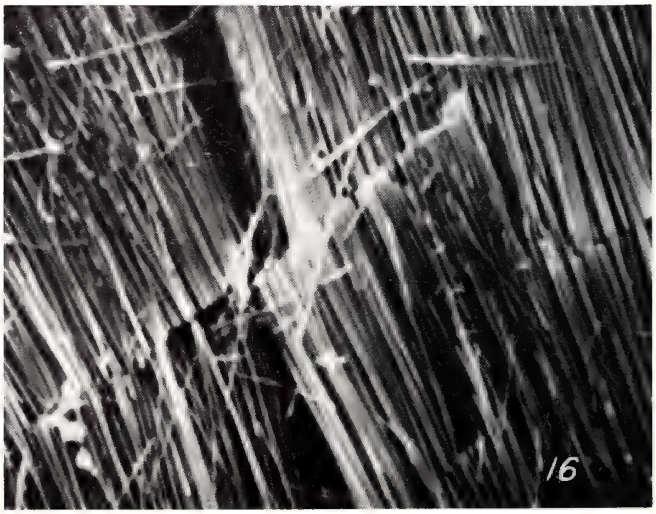


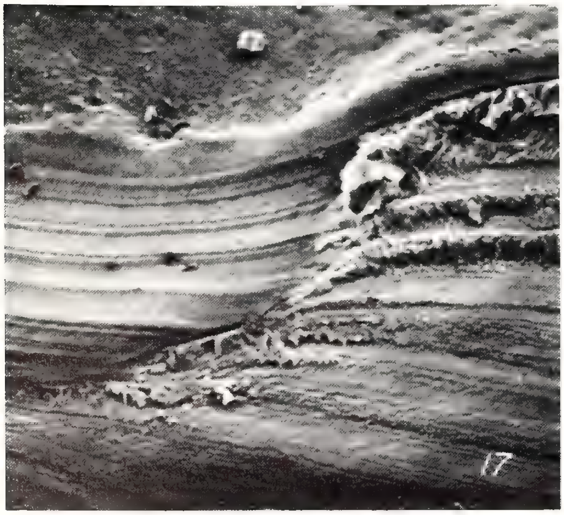
Fig. 7. Mantle-facing surface and fracture of foliated structure of left valve ventral to adductor muscle. Horizontal field width = 80 μm. **Fig. 8.** Mantle-facing surface of foliated structure of left valve at umbonal region. Horizontal field width = 80 μm. **Fig. 9.** Mantle-facing surface of chalky shell in left valve at umbonal region. Horizontal field width = 80 μm. **Fig. 10.** Fracture of chalky shell at right angles to mantle surface. Horizontal field width = 80 μm. **Fig. 11.** Surface of part of adductor muscle scar in right valve, adductor muscle removed with Clorox. Foliated structure at upper left. Prominent lines on scar indicate growth marks. Horizontal field width = 5 μm. **Fig. 12.** Surface of transitional zones (Mantle-facing) on ventral side of adductor muscle scar of left valve; scar, upper left; foliated structure, lower right; pebbly transitional zone in between. Horizontal field width = 150 μm.

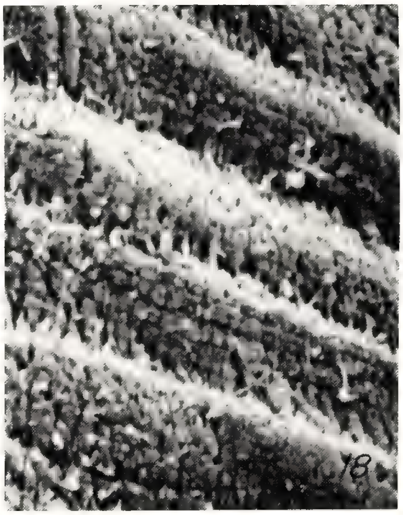












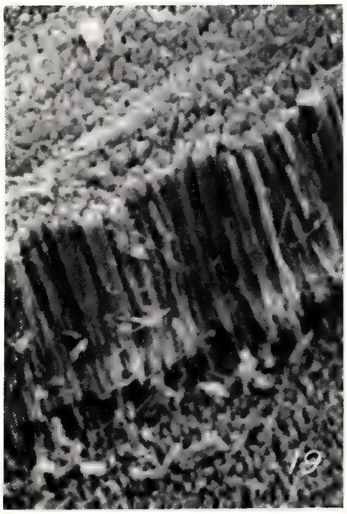


Fig. 13. Interior view of hinge line. Resilium, center; tensilia to left and right of resilium. Right valve, top; left valve, bottom. Horizontal field with = 5 μm. **Fig. 14.** Parts of resilium and anterior tensilium, interior view. Horizontal field width = 1.2 μm. **Fig. 15.** Resilium of ligament fractured parallel to length of aragonitic fibers and at right angles to growth strata. Horizontal field width = 80 μm. **Fig. 16.** Aragonitic fibers exposed by dissolution with Clorox of organic matrix of resilium. Horizontal field width = 40 μm. **Fig. 17.** Chondrophore (left) and anterior nympha (right) of right valve. Umbo is to bottom of micrograph, and mantle space is to top. Fragments of tensilium are still attached to nympha. Lines indicate growth increments. Horizontal field width = 4 μm. **Fig. 18.** Growth bands in ligostracum of nympha of left valve. Treatment with Clorox exposed individual prisms. Horizontal field with = 45 μm. **Fig. 19.** Fracture of ligostracum of nympha of right valve showing individual prisms. Horizontal field width = 40 μm.

Venezuela (Ahmed, 1975). The close morphological similarity of the three southern taxa suggests that they may simply be ecological variants or ecophenotypes (Mayr, 1969) evolving at the southern-most part of the range of *C. virginica* (Ahmed, 1975). It is likely that these ecophenotypes represent early stages of "becoming species" through geographic speciation, a process, however, that may be reversing itself as man accelerates the shipping of populations from one geographic region to another thereby speeding the mixing of different populations.

The close macromorphological similarity of the valves of *C. virginica, C. rhizophorea, C. guyenensis,* and *C. lacerata,* and the broad plasticity of the group, resulting in a wide range of variability in shell characters within each taxon, makes it difficult to separate them taxonomically. The question, then, may be logically asked if they are indeed separate species. Galtsoff (1964) concluded that although size, shape, curvature, and proportion of the umbones of the shell of oysters are useful generic characters, they cannot be entirely depended upon for taxonomic identification. The diffuseness of characters given by McLean (1941), Galtsoff (1964), and Abbott (1974) for taxonomic separation of *C. virginica* and *C. rhizophorae* attest the difficulties of identification at the species level.

The ultrastructural similarity of the valves of *Crassostrea virginica* and *C. rhizophorae* reported in this paper, especially in view of Carter's (1980) hypothesis that microstructure, as well as macrostructural variations in shell mineralogy and architecture, are largely biologically controlled, suggests a close systematic relationship of the two populations, and emphasizes the incipiency of the speciation of *C. rhizophorae*. So far as we could determine differences in the ultrastructure of shells of *C. rhizophorae* and *C. virginica* fell within the range of variation normally encountered within a single population of *C. virginica,* Carriker et al. (1980). Menzel (1972, 1973), as a result of ease of crossing, rearing of larvae through metamorphosis, chromosomal behavior, and morphological similarity, concluded tentatively that *C. rhizophorae* is a subspecies of *C. virginica*. The work of Rodriguez–Romero (1979) on karyotypes and Buroker et al. (1979) on genetic similarity likewise supports the close taxonomic proximity of the two taxa. In view of the difficulty of easily separating the two populations taxonomically, we suggest that *C. rhizophorae* be considered an ecotype of *C. virginica,* and not a separate species. Final determination of this matter will have to await further research.

In view of the plasticity of oysters and the influence of environmental factors on shell form, we were careful to compare young oysters of both *Crassostrea virginica* and *C. rhizophorae* that had set and grown on a smooth plastic surface. Thus substratum, which strongly influences macroform (Galtsoff, 1964; Palmer and Carriker, 1979), can be ruled out as a factor influencing the ultrastructure of the valves we studied. For reasons of expedience, our study of the ultrastructure of the valves of *C. rhizophorae* was limited to oysters ranging in height from 1.2 to 2.3 cm. Other studies on *C. virginica* (Carriker and Palmer, 1979; Carriker et al., 1980) indicate that the ultrastructure of the shell units and layers does not change appreciably as oysters increase in size.

Although speciation and the accurate identity of species of oysters is of considerable interest to biologists, it is also of significance to oyster growers. First, it is important to know the accurate name of species or subspecies of the oyster that is being cultivated so that it can be marketed with a correct name. Second, it is significant information in assessing the hybrid potential of controversial taxa of oysters in selective hybridization and in interpreting the significance of failures or successes of these (Ahmed, 1975; Longwell and Stiles, 1973). Third, the close similarity of *C. virginica* and *C. rhizophorae* offers a major benefit in the cultivation of *C. rhizophorae,* Nikolic et al. (1976), in that maximum use can be made of the technology of cultivation that has already been demonstrated efficient in the culture of *C. virginica* (Newball and Carriker, 1983).

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THE MOLLUSCAN FAUNA OF THE ELK RIVER IN TENNESSEE AND ALABAMA

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ABSTRACT

This survey was part of an intensive effort to document the Cumberlandian mussel fauna from tributary streams located in the southern Appalachian Mountains and the Cumberland Plateau region. Approximately 201 km (125 miles) of the Elk River was float-surveyed by boat using snorkeling and scuba-diving sampling techniques. Thirty-eight species of freshwater mussels, including 11 Cumberlandian forms and six species of river snails, were found living in the Elk River. Isom's (1973) preimpoundment mussel survey of the Elk River from 1965 to 1967 documented 35 species of freshwater mussels at one collecting site immediately below Tim's Ford Dam. Closure of Tim's Ford Dam in December 1970 has significantly affected the molluscan fauna below the dam. During our present survey, only one live species of river snail was found for a distance of almost 13 km (8 miles) below the dam.

The Elk River, located in south-central Tennessee, flows from the western edge of the Cumberland Plateau in Grundy County westward, where it joins the Tennessee River in Wheeler Reservoir. The Elk is 321.8 km (200 miles) long, of which 201.1 km (125 miles) is unimpounded.

The Elk River, including tributary streams, drains approximately 868 km^2 (2,249 square miles) through three geologic subdivisions: (1) the Cumberland Plateau, (2) the Highland Rim, and (3) the Central Basin. These geological subdivisions are all sedimentary in origin and consist principally of limestones and shales.

Two sizable impoundments are located on the Elk River: at 273.5 km, Wood's Reservoir, and at 212.4 km, Tim's Ford Reservoir. Both of these reservoirs are located in Franklin County, Tennessee. Wood's Dam, built by the Army Corps of Engineers between 1950 and 1952 and operated by the Arnold Engineering Development Center as a water supply reservoir, impounds approximately 19.3 km (12 miles) of the Elk River. Tim's Ford Dam, built by the Tennessee Valley Authority between 1966 and 1970, is operated by TVA for flood control, water supply, and power generation impounds an additional 54.7 km (34 miles) of the Elk. In addition, the lower 49.9 km (31 miles) of the Elk River in Limestone County, Alabama, is inundated by backwaters of Wheeler Reservoir, a mainstream impoundment on the Tennessee River operated by the Tennessee Valley Authority for navigation and flood control.

The Elk is one of several major tributary streams that form the headwaters of the Tennessee River system. These tributary streams, associated with the southern Appalachian Mountains and the Cumberland Plateau region, contain a rich assemblage of freshwater mussels endemic to the Tennessee drainage. Ortmann (1925) referred to these species as the Cumberlandian fauna. Surveys conducted in 1924 (Remington and Clench, 1925), 1925 (Ortmann, 1925), and from 1965 to 1967 (Isom et al., 1973) documented the presence of a total of 61 species of freshwater mussels and 5 species of river snails occurring in the Elk River.

This paper presents the results of a 1980 Elk River dive-float survey for freshwater mussels that was part of a broader survey of the Cumberlandian mussel fauna in Tennessee River tributary streams designed to provide information for TVA's Cumberlandian Mollusk Conservation Program.

METHODS AND MATERIALS

From June through September 1980, the Elk River was floated between access points using canoes and flat bottom river boats. Each riffle or gravel shoal encountered was sampled for freshwater mussels and snails, as were the pool areas at the head of each shoal. Each site was sampled using wading, snorkeling, and scuba diving sampling techniques. Approximately four to five divers were utilized during this survey, and average time spent for each person sampling per shoal was estimated at between 45 and 60 minutes. All freshwater mussels were identified in the field, and representative voucher specimens of mussels and snails were returned to the laboratory for positive identification, enumera-

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tion, and storage at TVA's fisheries laboratory at Norris, Tennessee. A total of 108 collecting sites representing a distance of almost 201 km (125 river miles) was sampled (Table 1, Fig. 1).

Table 1. Location of all Elk River collecting sites in kilometers (km) and river miles (ERM) and number of live mollusk species found at each site, June–September 1980.

Site	km	Elk River mile	Number of Species
1	45.1	28.0 (Gallus Island—Limestone Co., AL)	6
2	50.2	31.2 (Mason Island—Limestone Co., AL)	8
3	55.9	34.8 (Giles, Co., TN)	14
4	59.8	37.2 (Whitfield Island—Giles Co., TN)	12
5	66.5	41.3 (Ward Bluff—Giles Co., TN)	2
6	72.1	44.8 (Giles Co., TN)	14
7	72.9	45.3 (Above Holland Creek—Giles Co., TN)	8
8	76.1	47.3 (Giles Co., TN)	8
9	80.5	50.0 (Giles Co., TN)	6
10	82.1	51.0 (Persimmon Island—Giles Co., TN)	7
11	86.9	54.0 (Below RR crossing—Giles Co., TN)	11
12	89.8	55.8 (Lincoln Co., TN)	10
13	93.3	58.0 (Lincoln Co., TN)	8
14	94.9	59.0 (Mitchell Bend—Lincoln Co., TN)	8
15	96.5	60.0 (Lincoln Co., TN)	9
16	104.6	65.0 (Below Carr Creek—Lincoln Co., TN)	4
17	110.5	68.7 (Hovis Bend Island—Lincoln Co., TN)	8
18	113.0	70.2 (Below Moline Creek—Lincoln Co., TN)	2
19	113.4	70.5 (Lincoln Co., TN	22
20	115.2	71.6 (Island at Pearl City—Lincoln Co., TN)	8
21	115.8	72.0 (Lincoln Co., TN)	8
22	118.7	73.8 (Lincoln Co., TN)	10
23	119.9	74.5 (Lincoln Co., TN)	14
24	121.5	75.5 (Island above Dry Creek—Lincoln Co., TN)	13
25	123.1	76.5 (Bridge crossing—Lincoln Co., TN)	14
26	126.6	78.7 (Lincoln Co., TN)	21
27	127.1	79.0 (Lincoln Co., TN)	5
28	130.0	80.8 (Pitts Bend Island—Lincoln Co., TN)	4
29	131.1	81.5 (Lincoln Co., TN)	14
30	131.9	82.0 (Suggs Bend—Lincoln Co., TN)	8
31	132.7	82.5 (Lincoln Co., TN)	5
32	133.5	83.0 (Lincoln Co., TN)	10
33	134.4	83.5 (Morgan Bend—Lincoln Co., TN)	5
34	136.8	85.0 (Lincoln Co., TN)	11
35	137.7	85.6 (Lincoln Co., TN)	1
36	140.3	87.2 (Above Cane Creek—Lincoln Co., TN)	5
37	140.9	87.6 (Lincoln Co., TN)	0
38	147.2	91.5 (Above Fayetteville—Lincoln Co., TN)	20
39	148.7	92.4 (Above Wells Creek—Lincoln Co., TN)	13
40	149.6	93.0 (Henry Bend—Lincoln Co., TN)	9
41	150.8	93.7 (Below Eldad Bridge—Lincoln Co., TN)	5
42	151.7	94.3 (Lincoln Co., TN)	5
43	152.1	94.5 (Lincoln Co., TN)	6
44	153.2	95.2 (Island at Lucinda Bend—Lincoln Co., TN)	5
45	154.5	96.0 (Above Lucinda Bend—Lincoln Co., TN)	16
46	155.4	96.6 (Lincoln Co., TN)	0
47	157.4	97.8 (Lincoln Co., TN)	11
48	158.8	98.7 (Lincoln Co., TN)	8
49	160.9	100.0 (Lincoln Co., TN)	7
50	162.0	100.7 (Lincoln Co., TN)	10
51	162.8	101.2 (Below Mulberry Creek—Lincoln Co., TN)	9
52	165.4	102.8 (Above Mulberry Creek—Lincoln Co., TN)	7
53	167.3	104.0 (Below Cowley Bridge—Lincoln Co., TN)	12
54	167.8	104.3 (At Dukes Creek—Lincoln Co., TN)	11
55	168.9	105.0 (Above Stephens Creek—Lincoln Co., TN)	11
56	169.3	105.2 (Lincoln Co., TN)	9
57	169.6	105.4 (Below Dickey Bridge—Lincoln Co., TN)	11
58	171.4	106.5 (Pitts Bend—Lincoln Co., TN)	19
59	172.8	107.4 (Dickey Island—Lincoln Co., TN)	11
60	176.5	109.7 (Lincoln Co., TN)	16
61	177.2	110.1 (Below Shelton Creek—Lincoln Co., TN)	5
62	177.3	110.2 (Lincoln Co., TN)	8
63	180.4	112.1 (Lincoln Co., TN)	13
64	181.0	112.5 (Shiloh Bridge—Lincoln Co., TN)	12
65	182.9	113.7 (Stiles Ford—Lincoln Co., TN)	13
66	183.6	114.1 (Lincoln/Moore Cos., TN)	6
67	184.4	114.6 (Lincoln/Moore Cos., TN)	2
68	184.7	114.8 (Sullenger Bend—Lincoln/Moore Cos., TN)	8
69	185.7	115.4 (Lincoln/Moore Cos., TN)	1
70	190.3	118.3 (Parks Island—Lincoln/Moore Cos., TN)	18
71	192.0	119.3 (Old Pam Ford—Lincoln/Moore Cos., TN)	9
72	193.1	120.0 (Below Beans Creek—Lincoln/Moore Cos., TN)	1
73	194.4	120.8 (Moore/Franklin Cos., TN)	6
74	195.0	121.2 (Cashion Bend—Moore/Franklin Cos., TN)	5
75	197.6	122.8 (Island below gauging station—Moore/Franklin Cos., TN)	1
76	199.5	124.0 (Smith Island—Moore/Franklin Cos., TN)	4
77	203.4	126.4 (Moore/Franklin Cos., TN)	1
78	210.5	130.8 (Garner Ford—Franklin Cos., TN)	0
79	211.6	131.5 (Franklin Co., TN)	1
80	212.4	132.0 (Below Tim's Ford Dam—Franklin Co., TN)	0

Table 1. Continued.

Site	km	Elk River mile	Number of Species
81	270.3	168.0 (Franklin Co., TN)	0
82	270.8	168.3 (Franklin Co., TN)	1
83	271.1	168.5 (Franklin Co., TN)	0
84	272.7	169.5 (Wood's Reservoir Dam—Franklin Co., TN)	4
85	300.9	187.0 (Franklin/Coffee Cos., TN)	8
86	301.4	187.3 (Rutledge Ford—Franklin/Coffee Cos., TN)	5
87	301.7	187.5 (Franklin/Coffee Cos., TN)	0
88	302.2	187.8 (Franklin/Coffee Cos., TN)	3
89	303.3	188.5 (Above Mud Creek—Franklin/Coffee Cos., TN)	1
90	304.1	189.0 (Above Betsy Willis Creek—Franklin/Coffee Cos., TN)	2
91	306.2	190.3 (Bluebell Island—Franklin Cos., TN)	6
92	307.6	191.2 (Grundy Co., TN)	5
93	308.1	191.5 (Grundy Co., TN)	1
94	308.6	191.8 (Below Patton Creek—Grundy Co., TN)	2
95	309.2	192.2 (Below I-24 Bridge—Grundy Co., TN)	5
96	310.4	192.9 (Above Caldwell Creek—Grundy Co., TN)	4
97	310.9	193.2 (Grundy Co., TN)	4
98	311.5	193.6 (Ford at Bells Mill—Grundy Co., TN)	4
99	312.1	194.0 (Below Highway 41 Bridge—Grundy Co., TN)	2
100	313.0	194.5 (Above Highway 41 Bridge—Grundy Co., TN)	5
101	313.6	194.9 (Grundy Co., TN)	6
102	313.9	195.1 (Grundy Co., TN)	4
103	316.2	196.5 (Grundy Co., TN)	4
104	316.8	196.9 (Grundy Co., TN)	4
105	318.6	198.0 (Grundy Co., TN)	3
106	320.5	199.2 (Below Sartain Spring—Grundy Co., TN)	4
107	321.0	199.5 (Above Sartain Spring—Grundy Co., TN)	3
108	321.8	200.0 (Burrow Cove—Grundy Co., TN)	3

RESULTS AND DISCUSSION

Live or freshly dead specimens of 38 species of freshwater mussels including 11 Cumberlandian forms and six species of river snails were found during this survey (Table 2). Four of the 11 Cumberlandian species (*Conradilla caelata, Fusconaia cuneolus, Fusconaia edgariana,* and *Quadrula intermedia*) are listed as endangered by the U.S. Fish and Wildlife Service.

Eleven species of freshwater mussels were found in the upper Elk River above Wood's Dam Reservoir between sites 85 and 108. This portion of the Elk is heavily impacted by sand and silt runoff from adjacent farmlands. Collecting sites immediately below Wood's Dam Reservoir sites 81–84 were practically devoid of any living mussels. This portion of the Elk is affected by water releases from Wood's Dam and a landfill project adjacent to the river. Only two species of mussels (*Elliptio dilatatus* and *Villosa nebulosa*) represented by one specimen each were found.

Collecting sites closest to Tim's Ford Dam between sites 77 and 80 produced no live mussels. Numerous dead shells and large areas of unstable, shifting substrate were observed in this section of the Elk. In comparison, Isom et al. (1973) collected 34 species of freshwater mussels directly below the construction site at Tim's Ford Dam (presently site 80) between 1965 and 1967.

Isom et al. (1973) stated that "the mussel fauna downstream from Tim's Ford Dam will survive only if conditions for a warm water fishery are met." As a storage impoundment with a hypolimnal discharge, Tim's Ford Dam causes the river downstream to differ significantly from both preimpoundment conditions in the same area [and] from comparable unregulated stream reaches above the reservoir. These postimpoundment differences include altered temperature regimes, extreme water-level fluctuations, and seasonal oxygen deficits. Biological responses attributable to these environmental changes typically include reduced fish and benthic macroinvertebrate communities that can tolerate these conditions (Isom, 1971). Further, changes or reductions in the fish fauna

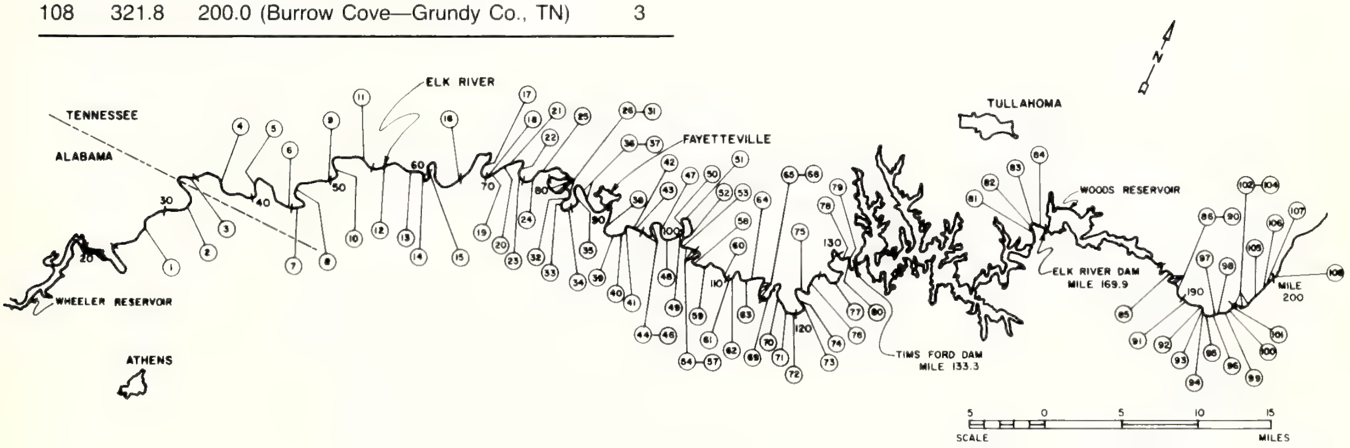

Table 2. Number of each mollusk species found during qualitative sampling of the Elk River, June through September 1980.

				COLLECTING SITES																			
Species	Ortmann (1925)	Isom (1973)	Ahlstedt (1980)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Mussels:																							
Actinonaias carinata	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Actinonaias pectorosa+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Alasmidonta minor (=calceolus)+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Alasmidonta marginata	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Amblema costata (=plicata)	X	X	X	-	1	3	-	-	-	-	-	-	-	-	-	1	-	-		-	-	-	-
Anodonta grandis	-	X	X	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-		-	-	-	-
Carunculina lividus (=moesta)+	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Carunculina moesta+	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Carunculina moesta f. *cylindrella*+*	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Conradilla caelata+*	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	1	-
Corbicula manilensis	-	X	X	-	-	-	3	-	9	-	1	3	11	2	2	-	1	3		2	-	1	2
Cyclonaias tuberculata	-	X	X	-	1	5	2	-	31	1	1	-	1	3	4	5	1	-		5	-	62	1
Dromus dromas+*	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia biemarginata+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia brevidens+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia capsaeformis+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia florentina+*	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia haysiana+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
*Dysnomia torulosa**	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Dysnomia triquetra	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Elliptio crassidens	-	X	X	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-		-	-	1	1
Elliptio dilatatus	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Fusconaia barnesiana+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	N	-	-	1	-
Fusconaia barnesiana f. *bigbyensis*+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	-	-
Fusconaia cuneolus+*	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	1	-
Fusconaia edgariana+*	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M	-	-	1	-
Fusconaia subrotunda	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	U	-	-	-	-
Lampsilis anodontoides	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	-	-
Lampsilis fasciola	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	S	1	-	1	-
Lampsilis ovata	-	X	X	-	-	-	-	-	3	1	-	-	-	1	-	-	-	-	E	-	-	1	-
Lampsilis ovata ventricosa	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-
Lasmigona complanata	-	X	X	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	-	-
Lasmigona costata	X	X	X	-	-	-	-	-	2	-	-	-	-	2	-	-	-	-		-	-	3	-
Lastena lata	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Leptodea fragilis	-	X	X	4	2	10	5	4	-	-	-	1	-	-	-	-	-	1		-	-	-	-
Lexingtonia dolabelloides+	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	23	-
Lexingtonia dolabelloides f. *conradi*+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Medionidus conradicus+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Megalonaias gigantea	-	X	X	-	-	7	5	-	10	-	-	-	-	3	1	-	-	-		1	-	33	1
Obliquaria reflexa	-	X	X	1	-	2	-	-	1	-	1	-	-	-	-	-	-	-		-	1	4	-
Obovaria subrotunda	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	1	-
Obovaria subrotunda f. *lens*	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pegias fabula+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Plagiola lineolata	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	16	-
Pleurobema cordatum	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pleurobema oviforme+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pleurobema oviforme f. *argenteum*+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Proptera alata	-	X	X	7	-	3	6	4	2	2	-	-	2	1	3	1	-	1		-	-	1	-
Ptychobranchus fasiolaris	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Ptychobranchus subtentum+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Quadrula cylindrica	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Quadrula intermedia+*	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	2	-
Quadrula metanevra	-	X	X	-	-	1	-	-	3	1	-	-	-	-	-	1	-	1		-	-	6	-
Quadrula pustulosa	-	X	X	-	-	-	-	-	4	-	-	-	-	1	2	1	1	-		-	1	61	-
Quadrula quadrula	-	X	X	-	1	3	1	-	-	-	-	-	-	-	1	-	-	-		-	-	-	-
Strophitus rugosus (=undulatus)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Tritogonia verrucosa	X	X	X	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Truncilla donaciformis	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Truncilla truncata	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa fabalis	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa iris	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa nebulosa+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa taeniata+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa vanuxemi+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa sp.	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Total Number of Mussel Species				3	4	10	8	2	10	4	4	2	3	7	6	5	4	4		4	2	19	4
Snails:																							
Anculosa (=Leptoxis) praerosa				1	83	157	110	-	200	148	98	114	81	261	77	624	36	243	186	64	-	38	81
Campeloma sp.				-	-	-	-	-	-	-	-	1	3	-	-	-	-	1	-	-	-	-	-
Goniobasis sp.				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata				12	80	4	17	-	32	1	29	1	84	32	60	33	6	11	11	54	-	-	2
Lithasia (=Io) verrucosa lima				-	17	130	243	-	183	182	50	96	146	281	133	257	22	108	222	101	-	74	100
Pleurocera canaliculatum				54	14	36	5	-	40	8	81	-	51	47	91	-	14	2	71	27	-	52	11
Total Number of Snail Species				3	4	4	4	0	4	4	4	4	4	4	4	3	4	5	4	4	0	3	4

+Cumberlandian Forms
*Endangered Species

												COLLECTING SITES																				
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
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-	-	-	5	1	-	-	-	1	-	1	-	-	1				38	14	-	1	2	2	4	18		11	5	3	16	1	4	11
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4	6	9	13	11	19	2	2	10	5	4	7	3	8				15	9	7	2	2	5	3	12		8	7	5	6	6	5	9
48	7	1	-	19	-	9	-	1	70	-	104	-	-	1	1	-	132	12	-	9	-	1	73	4	-	-	-	-	9	-	-	-
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4	2	1	-	-	-	-	-	1	-	-	-	-	1	-	8	-	48	36	-	-	2	-	-	2	-	1	-	-	4	41	-	1
139	20	5	-	32	-	54	1	31	134	1	179	2	3	-	1	-	410	51	9	92	14	-	176	71	-	3	-	30	15	2	15	8
89	23	170	-	16	1	223	-	65	16	-	172	3	9	-	1	-	199	180	33	1	37	-	-	72	-	28	4	4	10	3	1	5
4	4	4	0	3	2	3	2	4	3	1	3	2	3	1	5	0	5	4	2	3	3	1	2	4	0	3	1	2	4	3	2	3

Table 2. Number of each mollusk species found during qualitative sampling of the Elk River, June through September 1980.

				COLLECTING SITES																		
Species	Ortmann (1925)	Isom (1973)	Ahlstedt (1980)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Mussels																						
Actinonaias carinata	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Actinonaias pectorosa+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Alasmidonta minor (=calceolus)+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Alasmidonta marginata	X	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Amblema costata (=plicata)	X	X	X	-	1	1	-	-	-	-	-	-	-	-	-	1	-	-		-	-		-
Anodonta grandis	-	X	X	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-		-	-		-
Carunculina lividus (=moesta)+		-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Carunculina moesta+	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Carunculina moesta f. cylindrella+*	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Conradilla caelata+*	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Corbicula manilensis	-	X	X	-	-	-	3	-	9	-	1	3	11	2	2	-	1	3		2	-		2
Cyclonaias tuberculata	-	X	X	-	1	5	2	-	31	1	1	-	1	3	4	5	1	-		5	-	1	1
Dromus dromas+*	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia biemarginata+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia brevidens+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia capsaeformis+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia florentina+*	-	X		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia haysiana+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia torulosa*	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Dysnomia triquetra		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Elliptio crassidens	-	X	X	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-		-	-		1
Elliptio dilatatus	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Fusconaia barnesiana+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	N	-	-		-
Fusconaia barnesiana f. bigbyensis+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-		-
Fusconaia cuneolus+*	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-
Fusconaia edgariana+*	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	M	-	-		-
Fusconaia subrotunda			X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	U	-	-		-
Lampsilis anodontoides	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-		-
Lampsilis fasciola	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	S	1	-		-
Lampsilis ovata	-	X	X	-	-	-	-	-	3	1	-	-	-	1	-	-	-	-	E	-	-	1	-
Lampsilis ovata ventricosa	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-		-
Lasmigona complanata	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	-	-
Lasmigona costata	X	X	X	-	-	-	-	-	2	-	-	-	-	2	-	-	-	-		-	-	-	-
Lastena lata	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Leptodea fragilis		X	X	4	2	10	5	4	-	-	-	1	-	-	-	-	-	1		-	-	-	-
Lexingtonia dolabelloides+		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Lexingtonia dolabelloides f. conradi+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Medionidus conradicus+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Megalonaias gigantea	-	X	X	-	-	7	5	-	10	-	-	-	-	3	1	-	-	-		1	-	5	1
Obliquaria reflexa	-	X	X	1	-	2	-	-	1	-	1	-	-	-	-	-	-	-		-	-	-	-
Obovaria subrotunda		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Obovaria subrotunda f. lens	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pegias fabula+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Plagiola lineolata		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	16	-
Pleurobema cordatum		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pleurobema oviforme+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Pleurobema oviforme f. argenteum+	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Proptera alata	-	X	X	7	-	3	6	4	2	2	-	-	2	1	3	1	-	1		-	-	1	-
Ptychobranchus fasiolaris	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Ptychobranchus subtentum+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Quadrula cylindrica	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Quadrula intermedia+*		X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	2	-
Quadrula metanevra	-	X	X	-	-	1	-	-	3	1	-	-	-	-	-	1	-	1		-	-	6	-
Quadrula pustulosa		X	X	-	-	-	-	-	4	-	-	-	-	1	2	1	1	-		-	1	61	-
Quadrula quadrula		X	X	-	1	3	-	-	-	-	-	-	-	-	1	-	-	-		-	-	-	-
Strophitus rugosus (=undulatus)	X	X		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Tritogonia verrucosa	X	X	X	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Truncilla donaciformis	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Truncilla truncata		X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa fabalis	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa iris	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa nebulosa+	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa taeniata+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa vanuxemi+	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Villosa sp	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
Total Number of Mussel Species				3	4	10	8	2	10	4	4	2	3	7	6	5	4	4		4	2	19	4
Snails																						
Anculosa (=Leptoxis) praerosa				1	83	157	110	-	200	148	98	114	81	261	77	624	36	243	186	64	-	38	81
Campeloma sp				-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-
Goniobasis sp				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata				12	80	4	17	-	32	1	29	1	84	32	60	33	6	11	11	54	-	-	2
Lithasia (=Io) verrucosa lima				-	17	130	243	-	183	182	50	96	146	281	133	257	22	108	222	101	-	74	100
Pleurocera canaliculatum				54	14	36	5	-	40	8	81	-	51	47	91	-	14	2	71	27	-	52	11
Total Number of Snail Species				3	4	4	4	0	4	4	4	4	4	4	4	3	4	5	4	4	0	3	4

	COLLECTING SITES																																
Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Mussels																																	
Actinonaias carinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Actinonaias pectorosa+	-	-	-	5	1	-	-	-	1	-	1	-	-	1				38	14	-	1	2	2	4	18		11	5	3	16	1	4	11
Alasmidonta minor (=calceolus)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Alasmidonta marginata	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Amblema costata (=plicata)	-	2	2	3	-	-	-	-	-	-	-	-	-	-				-	1	2	-	-	-	-	-		-	-	-	-	-	-	-
Anodonta grandis	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Carunculina lividus (=moesta)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Carunculina moesta+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Carunculina moesta f. cylindrella+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Conradilla caelata+*	-	-	-	-	-	-	-	-	-	-	-	1	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Corbicula manilensis	2	-	-	-	1	-	-	-	1	-	-	3	1	2				8	4	3	9	-	1	2	5		-	1	1	2	1	1	1
Cyclonaias tuberculata	4	5	3	29	6	5	-	-	10	1	-	2	-	-				41	22	2	-	4	1	-	7		24	9	8	5	1	1	9
Dromus dromas+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia biemarginata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia brevidens+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia capsaeformis+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia florentina+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia haysiana+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia torulosa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Dysnomia triquetra	-	-	-	-	-	1	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Elliptio crassidens	-	1	-	1	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Elliptio dilatatus	-	-	-	1	-	1	-	-	-	-	-	-	-	-				1	-	-	-	-	-	-	-		-	1	-	-	1	-	-
Fusconaia barnesiana+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	N	N	N	-	-	-	-	-	-	-	-	N	-	-	-	-	-	-	-
Fusconaia barnesiana f. bigbyensis+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	O	O	-	-	-	-	-	-	-	-	O	-	-	-	-	-	-	-
Fusconaia cuneolus+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Fusconaia edgariana+*	-	-	-	-	2	1	-	-	-	-	-	-	-	-	M	M	M	1	-	-	-	-	-	-	-	M	-	-	-	-	-	-	1
Fusconaia subrotunda	-	-	-	-	-	1	-	-	-	-	-	-	-	-	U	U	U	-	1	-	-	-	-	-	-	U	-	-	-	-	-	-	1
Lampsilis anodontoides	-	-	-	-	-	1	-	-	-	-	-	-	-	-	S	S	S	-	-	-	-	-	-	-	-	S	-	-	-	-	-	-	-
Lampsilis fasciola	-	-	-	-	-	2	-	-	-	-	-	-	-	-	S	S	S	1	-	-	-	-	-	-	-	S	-	-	-	-	-	-	-
Lampsilis ovata	-	-	-	5	-	1	-	-	2	2	2	1	1	1	E	E	E	9	3	1	-	-	-	-	1	E	4	2	1	2	-	-	4
Lampsilis ovata ventricosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	L	L	-	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-
Lasmigona complanata	-	-	-	-	-	1	-	-	-	-	-	-	-	-	S	S	S	-	-	-	-	-	-	-	-	S	-	-	-	-	-	-	-
Lasmigona costata	1	2	1	5	2	2	-	-	11	7	-	-	-	17				55	24	2	-	-	1	2	11		23	12	7	3	1	1	14
Lastena lata	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	1	-	-	-	-	-
Leptodea fragilis	-	-	-	-	-	1	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Lexingtonia dolabelloides+	-	1	1	-	-	2	-	-	2	-	2	-	-	-				4	2	2	-	-	2	-	9		-	-	-	1	4	-	-
Lexingtonia dolabelloides f. conradi+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Medionidus conradicus+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				1	-	-	-	-	-	-	2		-	-	-	-	-	-	-
Megalonaias gigantea	-	4	3	20	1	-	2	-	-	-	-	-	-	12				1	3	-	-	-	-	-	-		1	-	-	-	-	-	-
Obliquaria reflexa	-	-	-	2	1	2	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Obovaria subrotunda	-	-	-	-	-	1	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Obovaria subrotunda f. lens	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Pegias fabula+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Plagiola lineolata	-	-	1	-	-	1	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Pleurobema cordatum	-	-	-	-	-	-	-	-	1	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Pleurobema oviforme+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Pleurobema oviforme f. argenteum+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Proptera alata	-	-	-	3	8	4	-	-	1	2	-	-	-	3				1	-	-	-	-	-	-	1		4	-	-	-	-	-	-
Ptychobranchus fasiolaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Ptychobranchus subtentum+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Quadrula cylindrica	-	-	1	-	-	-	-	-	-	-	-	-	-	-				4	-	-	-	-	-	-	2		1	-	-	-	-	1	1
Quadrula intermedia+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-				1	-	-	-	-	-	-	1		1	-	-	-	-	-	-
Quadrula metanevra	-	-	-	-	-	2	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Quadrula pustulosa	2	-	1	8	1	19	-	1	2	-	-	1	-	12				4	-	1	-	-	-	-	4		-	-	-	-	-	-	-
Quadrula quadrula	-	-	1	1	1	26	11	5	2	2	1	1	1	5				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Strophitus rugosus (=undulatus)	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Tritogonia verrucosa	-	-	-	1	1	-	-	-	-	-	-	1	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Truncilla donaciformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Truncilla truncata	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa fabalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa iris	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa nebulosa+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa taeniata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa vanuxemi+	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Villosa sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-				-	-	-	-	-	-	-	-		-	-	-	-	-	-	-
Total Number of Mussel Species	4	6	9	13	11	19	2	2	10	5	4	7	3	8				15	9	7	2	2	5	3	12		8	7	5	6	6	5	9
Snails																																	
Anculosa (=Leptoxis) praerosa	48	7	1	-	19	-	9	-	1	70	-	104	-	-	1	1	-	132	12	-	9	-	1	73	4	-	-	-	-	9	-	-	-
Campeloma sp	-	-	-	-	-	10	-	1	-	-	-	-	-	-	-	1	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata	4	2	1	-	-	-	-	-	1	-	-	-	-	1	-	8	-	48	36	-	-	2	-	-	2	-	1	-	-	4	41	-	1
Lithasia (=Io) verrucosa lima	139	20	5	-	32	-	54	1	31	134	1	179	2	3	-	1	-	410	51	9	92	14	-	176	71	-	3	-	30	15	2	15	8
Pleurocera canaliculatum	89	23	170	-	16	1	223	-	65	16	-	172	3	9	-	1	-	199	180	33	1	37	-	-	72	-	28	4	4	10	3	1	5
Total Number of Snail Species	4	4	4	0	3	2	3	2	4	3	1	3	2	3	1	5	0	5	4	2	3	3	1	2	4	0	3	1	2	4	3	2	3

+Cumberlandian Forms
*Endangered Species

Table 2. Continued

	COLLECTING SITES																							
Species	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
Mussels:																								
Actinonaias carinata	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Actinonaias pectorosa+	4	17	3	4	33	3	18	2	1	6	11	8	-	1	4	1	27	37		5	-		2	
Alasmidonta minor (=calceolus)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Alasmidonta marginata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Amblema costata (=plicata)	-	1	-	-	-	-	8	-	-	-	-	1	-	-	-	-	3	-		-	-		-	
Anodonta grandis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Carunculina lividus (=moesta)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Carunculina moesta+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Carunculina moesta f. *cylindrella*+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Conradilla caelata+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Corbicula manilensis	-	-	-	-	-	1	3	2	2	2	1	1	1	-	3	-	3	5		-	3		1	
Cyclonaias tuberculata	5	20	12	11	20	3	31	-	5	7	6	5	1	3	1	-	15	6		4	1		-	
Dromus dromas+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia biemarginata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia brevidens+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia capsaeformis+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia florentina+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia haysiana+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
*Dysnomia torulosa**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Dysnomia triquetra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Elliptio crassidens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Elliptio dilatatus	-	-	-	-	2	1	6	-	-	1	-	-	-	-	-	-	4	-		1	-		-	
Fusconaia barnesiana+	1	2	1	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	N	-	-	N	-	N
Fusconaia barnesiana f. *bigbyensis*+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	O	-	O
Fusconaia cuneolus+*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Fusconaia edgariana+*	-	-	-	-	-	2	1	-	-	-	1	-	-	-	-	-	3	-	M	-	-	M	-	M
Fusconaia subrotunda	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-	U	-	-	U	-	U
Lampsilis anodontoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	S	-	S
Lampsilis fasciola	-	-	1	-	1	1	-	-	-	-	1	-	-	-	-	-	2	-	S	-	-	S	-	S
Lampsilis ovata	3	2	7	5	4	1	2	-	-	2	1	2	-	-	-	-	11	-	E	2	-	E	1	E
Lampsilis ovata ventricosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	L	-	L
Lasmigona complanata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	S	-	S
Lasmigona costata	8	23	25	13	17	-	11	-	1	4	-	11	1	-	1	-	17	10		1	-		-	
Lastena lata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Leptodea fragilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Lexingtonia dolabelloides+	1	3	3	4	5	-	8	-	-	4	2	4	-	-	-	-	4	4		3	1		-	
Lexingtonia dolabelloides f. *conradi*+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Medionidus conradicus+	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Megalonaias gigantea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Obliquaria reflexa	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Obovaria subrotunda	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	-		-	
Obovaria subrotunda f. *lens*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Pegias fabula+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Plagiola lineolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Pleurobema cordatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Pleurobema oviforme+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-		-	-		-	
Pleurobema oviforme f. *argenteum*+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Proptera alata	-	1	2	1	2	-	-	-	-	-	-	2	-	-	1	-	4	-		-	-		-	
Ptychobranchus fasiolaris	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	-		-	
Ptychobranchus subtentum+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula cylindrica	1	1	-	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula intermedia+*	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula metanevra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula pustulosa	1	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	1	-		-	-		-	
Quadrula quadrula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Strophitus rugosus (=undulatus)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Tritogonia verrucosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-		-	-		-	
Truncilla donaciformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Truncilla truncata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa fabalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa iris	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	1		-	
Villosa nebulosa+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa taeniata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa vanuxemi+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Total Number of Mussel Species	8	9	9	8	15	8	12	2	4	10	8	9	3	2	5	1	15	5		6	4		3	
Snails:																								
Anculosa (=Leptoxis) praerosa	-	-	-	-	4	-	2	1	1	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-
Campeloma sp.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata	1	-	-	2	30	38	10	27	103	32	149	240	10	-	150	-	75	90	5	-	111	44	232	80
Lithasia (=Io) verrucosa lima	18	26	-	16	37	32	60	138	24	23	98	1	15	-	2	-	14	2	-	-	-	-	-	-
Pleurocera canaliculatum	1	4	-	9	46	9	3	-	2	1	1	7	11	-	1	-	3	5	-	-	-	-	-	-
Total Number of Snail Species	3	2	0	3	4	3	4	3	4	3	4	4	3	0	3	0	3	4	1	0	1	1	1	1

+Cumberlandian Forms
*Endangered Species

COLLECTING SITES																														
78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
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Table 2. Continued

Species	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
	COLLECTING SITES																							
Mussels																								
Actinonaias carinata	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Actinonaias pectorosa+	4	17	3	4	33	3	18	2	1	[illegible]	11	8	-	1	4	1	27	37		5	-			
Alasmidonta minor (=*calceolus*)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Alasmidonta marginata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Amblema costata (=*plicata*)	-	1	-	-	-	-	8	-	-	-	-	1	-	-	-	-	3	-		-	-			
Anodonta grandis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Carunculina lividus (=*moesta*)+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Carunculina moesta+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Carunculina moesta f. *cylindrella*+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Conradilla caelata+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Corbicula manilensis	-	-	-	-	-	1	3	2	2	2	1	1	1	-	3	-	3	5		-	[illegible]			
Cyclonaias tuberculata	5	20	12	11	20	3	31	-	5	7	6	5	1	3	1	-	15	6		4	1			
Dromus dromas+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia biemarginata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia brevidens+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia capsaeformis+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia florentina+*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia haysiana+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
*Dysnomia torulosa**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Dysnomia triquetra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Elliptio crassidens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Elliptio dilatatus	-	-	-	-	2	1	6	-	-	1	-	-	-	-	-	-	4	-		1	-			
Fusconaia barnesiana+	1	2	1	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	N	-	-	N		N
Fusconaia barnesiana f. *bigbyensis*+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	O	-	-	O		O
Fusconaia cuneolus+*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Fusconaia edgariana+*	-	-	-	-	-	2	1	-	-	-	1	-	-	-	-	-	3	-	M	-	-	M		M
Fusconaia subrotunda	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-	U	-	-	U		U
Lampsilis anodontoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-		S		S
Lampsilis fasciola	-	-	1	-	1	1	-	-	-	-	1	-	-	-	-	-	2	-	S	-		S		S
Lampsilis ovata	3	2	7	5	4	1	2	-	-	2	1	2	-	-	-	-	11	-	E	2		E		E
Lampsilis ovata ventricosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	L		L
Lasmigona complanata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S	-	-	S		S
Lasmigona costata	8	23	25	13	17	-	11	-	1	4	-	11	1	-	1	-	17	10		1				
Lastena lata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-				
Leptodea fragilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-				
Lexingtonia dolabelloides+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Lexingtonia dolabelloides f. *conradi*+	1	3	3	4	5	-	8	-	-	4	2	4	-	-	-	-	4	4		3	1			
Medionidus conradicus+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Megalonaias gigantea	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Obliquaria reflexa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Obovaria subrotunda	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Obovaria subrotunda f. *lens*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	-			
Pegias fabula+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Plagiola lineolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Pleurobema cordatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Pleurobema oviforme+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Pleurobema oviforme f. *argenteum*+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-		-	-			
Proptera alata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Ptychobranchus fasciolaris	-	1	2	1	2	-	-	-	-	-	-	2	-	-	1	-	4	-		-	-			
Ptychobranchus subtentum+	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	-		-	
Quadrula cylindrica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula intermedia+*	1	1	-	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-		-				
Quadrula metanevra	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-		-				
Quadrula pustulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Quadrula quadrula	1	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	1	-		-	-		-	
Strophitus rugosus (=*undulatus*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Tritogonia verrucosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Truncilla donaciformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-		-				
Truncilla truncata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Villosa fabalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Villosa iris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Villosa nebulosa+	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-		-	1			
Villosa taeniata+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Villosa vanuxemi+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-			
Villosa sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-		-	
Total Number of Mussel Species	8	9	9	8	15	8	12	2	4	10	8	9	3	2	5	1	15	5		6	4		3	
Snails																								
Anculosa (=*Leptoxis*) *praerosa*	-	-	-	-	4	-	2	1	1	-	-	1	-	-	-	-	-	1	-	-		-	-	-
Campeloma sp	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-		-	
Goniobasis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata	1	-		2	30	38	10	27	103	32	149	240	10	-	150	-	75	90	5	-	111	44	232	80
Lithasia (=*Io*) *verrucosa lima*	18	26	-	16	37	32	60	138	24	23	98	1	15	-	2	-	14	2	-	-	-	-	-	-
Pleurocera canaliculatum	1	4	-	9	46	9	3	-	2	1	1	7	11	-	1	-	3	5	-	-	-	-	-	-
Total Number of Snail Species	3	2	0	3	4	3	4	3	4	3	4	4	3	0	3	0	3	4	1	0	1	1	1	1

+Cumberlandian Forms
*Endangered Species

Species	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
	COLLECTING SITES																														
Mussels																															
Actinonaias carinata					-		-	-	-		-	-	-		-	-		-	-	-	-	-	-	-	-	-	-	-	-		-
Actinonaias pectorosa+					-		-	-	-		-	-	-		-	-		-	-	-	-	-	-	-	-	-	-	-	-		-
Alasmidonta minor (=*calceolus*)+					-		-	-	-		-	-	-		-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alasmidonta marginata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amblema costata (=*plicata*)					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anodonta grandis					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carunculina lividus (=*moesta*)+					-		-	-	-		-	-	-	-	-	-		-	-	-	4	-	-	-	-	-	-	-	-	-	1
Carunculina moesta+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carunculina moesta f. *cylindrella*+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Conradilla caelata+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corbicula manilensis					-		5	5	10		4	-	2	4	-	-		4	-	-	-	16	1	2	-	-	5	11	6	2	16
Cyclonaias tuberculata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dromus dromas+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia biemarginata+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia brevidens+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia capsaeformis+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia florentina+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia haysiana+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Dysnomia torulosa**					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dysnomia triquetra					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elliptio crassidens					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elliptio dilatatus					-		1	-	-		-	-	-	1	-	-		-	-	-	-	-	-	-	-	-	-	-	3	6	-
Fusconaia barnesiana+	N	N	N	N	-	N	-	-	-	N	-	-	-	1	-	-	N	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fusconaia barnesiana f. *bigbyensis*+	O	O	O	O	-	O	-	-	-	O	-	-	-	-	-	-	O	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fusconaia cuneolus+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fusconaia edgariana+*	M	M	M	M	-	M	-	-	-	M	-	-	-	-	-	-	M	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fusconaia subrotunda	U	U	U	U	-	U	-	9	-	U	2	18	3	32	4	-	U	4	7	3	1	5	11	4	4	1	2	1	5	9	-
Lampsilis anodontoides	S	S	S	S	-	S	-	-	-	S	-	-	-	-	-	-	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampsilis fasciola	S	S	S	S	-	S	-	1	-	S	-	-	-	-	-	-	S	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Lampsilis ovata	E	E	E	E	-	E	-	-	-	E	-	-	-	-	-	-	E	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lampsilis ovata ventricosa	L	L	L	L	-	L	-	-	-	L	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lasmigona complanata	S	S	S	S	-	S	-	-	-	S	-	-	-	-	-	-	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lasmigona costata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lastena lata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptodea fragilis					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lexingtonia dolabelloides+					-		-	10	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lexingtonia dolabelloides f. *conradi*+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Medionidus conradicus+					-		-	-	-		-	-	-	-	2	-		-	-	-	1	-	-	7	2	-	-	-	-	-	-
Megalonaias gigantea					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Obliquaria reflexa					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Obovaria subrotunda					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Obovaria subrotunda f. *lens*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pegias fabula+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiola lineolata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurobema cordatum					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurobema oviforme+					-		-	2	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurobema oviforme f. *argenteum*+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Proptera alata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptychobranchus fasciolaris					-		-	2	-		-	-	-	-	-	-		1	-	-	-	-	2	-	-	-	-	-	-	-	-
Ptychobranchus subtentum+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula cylindrica					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula intermedia+*					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula metanevra					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula pustulosa					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quadrula quadrula					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strophitus rugosus (=*undulatus*)					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tritogonia verrucosa					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Truncilla donaciformis					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Truncilla truncata					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa fabalis					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa iris					1		-	5	1		3	-	-	-	32	5		1	1	2	6	1	5	10	33	3	3	2	7	11	12
Villosa nebulosa+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa taeniata+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa vanuxemi+					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Villosa sp					-		-	-	-		-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total Number of Mussel Species					1		2	7	2		3	1	2	4	3	1		4	3	3	4	2	4	5	4	3	3	2	3	3	2
Snails																															
Anculosa (=*Leptoxis*) *praerosa*	-	-	-	-	-	-	-	1	61	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campeloma sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniobasis laqueata	-	131	-	-	-	-	5	-	39	-	79	-	-	1	114	42	3	282	122	194	-	-	5	63	-	1	82	97	101	-	121
Lithasia (=*Io*) *verrucosa lima*	-	-	-	-	-	-	20	-	3	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleurocera canaliculatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total Number of Snail Species	0	1	0	0	0	0	2	1	3	0	3	0	0	2	2	1	2	1	1	1	0	0	1	1	0	1	1	1	1	0	1

indirectly affect the reproductive life cycle of freshwater mussels by eliminating potential host species.

The largest concentrations of mussels obseerved during this survey occurred in the lower reaches of the Elk River below site 74. Collecting sites 19 and 26 each contained 18 species of freshwater mussels, with 15 species found at site 58. The lowermost collecting site on the Elk River at 45 km (site 1) produced only three species of freshwater mussels (*Leptodea fragilis, Obliquaria reflexa,* and *Proptera alata*).

Seven species of freshwater mussels listed as endangered by the U.S. Fish and Wildlife Service had previously been reported from the Elk River. Three of these species, *Toxolasma (=Carunculina) cylindrellus, Dromus dromas,* and *Epioblasma (=Dysnomia) florentina),* were not found during this survey. However, living specimens of *Fusconaia cunelous, Fusconaia edgariana,* and *Quadrula intermedia* were found. *Conradilla caelata* was not found alive in the Elk River but was found freshly dead (with evidence of meat remaining in shell) from muskrat middens at sites 19 and 32. This is the first time *C. caelata* has been found in the Elk since Ortmann's 1925 survey.

Six species of river snails were found in the Elk River (Table 2). The greatest concentrations of snails occurred in the lower reaches of the Elk River below site 71. Dense concentrations of *Lithasia (=Io) verrucosa lima, Pleurocera canaliculatum, Goniobasis laqueata,* and *Anculosa (=Leptoxis) praerosa* were found at numerous sites on the Elk River. The snail fauna is especially sparse in the upper reaches of the Elk between sites 85 and 108 and below Wood's Dam site 84 and Tim's Ford Dam site 80. The disappearance of snails in these portions of the Elk may be attributable to the smallness of the stream in the upper headwaters, cold water temperatures originating from springs, operations of Tim's Ford and Wood's Dam, sand and silt runoff from agricultural land usages, and herbicide and pesticide spraying.

Freshwater mussels in the Elk River have been heavily impacted by water releases from Tim's Ford Dam. Numerous habitat is available for freshwater mussels as evidence by the numbers of gravel and sand shoals encountered while sampling, but a considerable amount of effort was required to find living mussels. In the lower reaches of the Elk below Fayetteville, Tennessee, hundreds of dead shells were observed buried in the substratum. This suggests a major, unknown, catastrophic event (chemical spill, outfall, etc.) that decimated the fauna. Freshwater mussels below Fayetteville are still surviving and could repopulate the lower reaches of the Elk, because these populations are far enough away from the immediate impacts caused by water releases from Tim's Ford Dam. However, these populations will survive only if the lower Elk River remains free from the pollution source that killed the hundreds of dead specimens observed.

ACKNOWLEDGMENT

I would like to take this opportunity to thank Karl T. Henn, W. Douglas Harned, and Steven R. Brown, biologists formerly with the Tennessee Valley Authority, for their help in conducting this survey, and Dr. David Stansbery, Ohio State University, Museum of Zoology, for his help in verifying specimens.

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NAIAD MOLLUSK POPULATIONS (BIVALVIA: UNIONIDAE) IN POOLS 7 AND 8 OF THE MISSISSIPPI RIVER NEAR LA CROSSE, WISCONSIN

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ABSTRACT

Since 1969 over 7,000 naiad mollusks have been collected from nine major and numerous minor sites in a 26 river-mile (41.8 km) section of the Upper Mississippi River near La Crosse, Wisconsin. Of importance was the 1977 identification of a juvenile endangered *Lampsilis higginsi* (Lea, 1857), the present-day northern–most live Mississippi River record of this species. Pool 7 had 21 live species and five species represented by empty shells, while Pool 8 had 22 live species and 15 species represented by empty shells, a total of 38 species (25 live and 13 represented by empty shells). Live *Anodonta suborbiculata* Say, 1831, *Potamilus ohiensis* (Rafinesque, 1820), *Toxolasma parvus* (Barnes, 1823), and subfossil *Pleurobema rubrum* (Rafinesque, 1820) were added to the list of 36 species recorded prior to 1931. The present total for Pools 7 and 8 (all known records) includes 30 living species and 10 species represented by empty shells. The overall total of 40 species compares favorably with the 46 recorded from the most diverse area of the Mississippi at Prairie du Chien, Wisconsin, 63 river miles (100.8 km) south of La Crosse. After comparing all known records from sites near La Crosse, it becomes apparent that the area no longer supports an overall flourishing naiad fauna except for a few species that are abundant in localized areas such as Lake Onalaska [*Amblema p. plicata* (Say, 1817), *Lampsilis ventricosa* (Barnes, 1823), *L. radiata luteola* (Lamarck, 1819), and the *Anodonta grandis* Say, 1829, complex] and near Isle la Plume [*Truncilla donaciformis* (Lea, 1827)]. *Toxolasma parvus* and *Pleurobema sintoxia* (Rafinesque, 1820), not common enough to be a regular part of the fauna in 1930, were found alive. *Anodonta imbecillis* Say, 1829, was often found in mud accumulated inside empty shells of other species.

Until recently the only known pre–1965 records of the naiad mollusk fauna of the La Crosse, Wisconsin, area of the Upper Mississippi River were the 28 species recorded in the Region III (present-day Pools 7, 8 and 9) of Ellis in 1930 (van der Schalie and van der Schalie, 1950) (Table 1). In 1907 Dr. Paul Bartsch of the U.S. National Museum (USNM), Smithsonian Institution, also conducted, but did not publish, a survey of mollusks of the Upper Mississippi River that included one site in the area now known as Pool 7 and six sites in the area now known as Pool 8. This part of the Mississippi River has been impounded since the construction of the nine-foot navigation channel in the mid-1930's (Fig. 1).

Unpublished records of Bartsch at USNM reveal 26 species for the present–day Pool 7 and 34 species for the present-day Pool 8, a total of 35 species. Ellis added *Anodonta imbecillis* Say, 1829, in 1930 to bring the pre-1965 total to 36 naiad species. Baker (1928) did not cite records of naiades from the La Crosse, Wisconsin, area.

In 1965 the Wisconsin Department of Natural Resources (Finke, 1966) conducted a mussel survey in five pools of the Upper Mississippi River bordering Wisconsin. Finke found 14 species living in Pool 7, but no survey work was done in Pool 8. In 1977–1979 the Wisconsin Department of Natural Resources conducted another survey in the Wisconsin portion of the Mississippi and found living individuals of 15 species (450 specimens) and the empty shells of 4 additional species in Pool 7 (Thiel, 1981). Living individuals of 15 species (239 specimens) and the empty shells of 8 additional species were found in Pool 8.

Fuller (1978, 1980a, 1980b) conducted site specific surveys in 1977–1979 for the St. Paul District, U.S. Army Corps of Engineers, St. Paul, Minnesota, in areas that were likely to be dredged to maintain the nine-foot navigation channel. This included four sites in Pool 7 and nine sites in Pool 8. Fuller found 13 species (173 specimens) living in Pool 7 and 20 species (757 specimens) living in Pool 8.

Mathiak (1979) hand collected at several sites in the La Crosse area and found seven species in Pool 7 and eight species in Pool 8. Coon et al. (1977) also collected from Pool 8 in 1975, but their data does not specify the number of sites collected or number of species found in Pool 8.

The objectives of this study were to:

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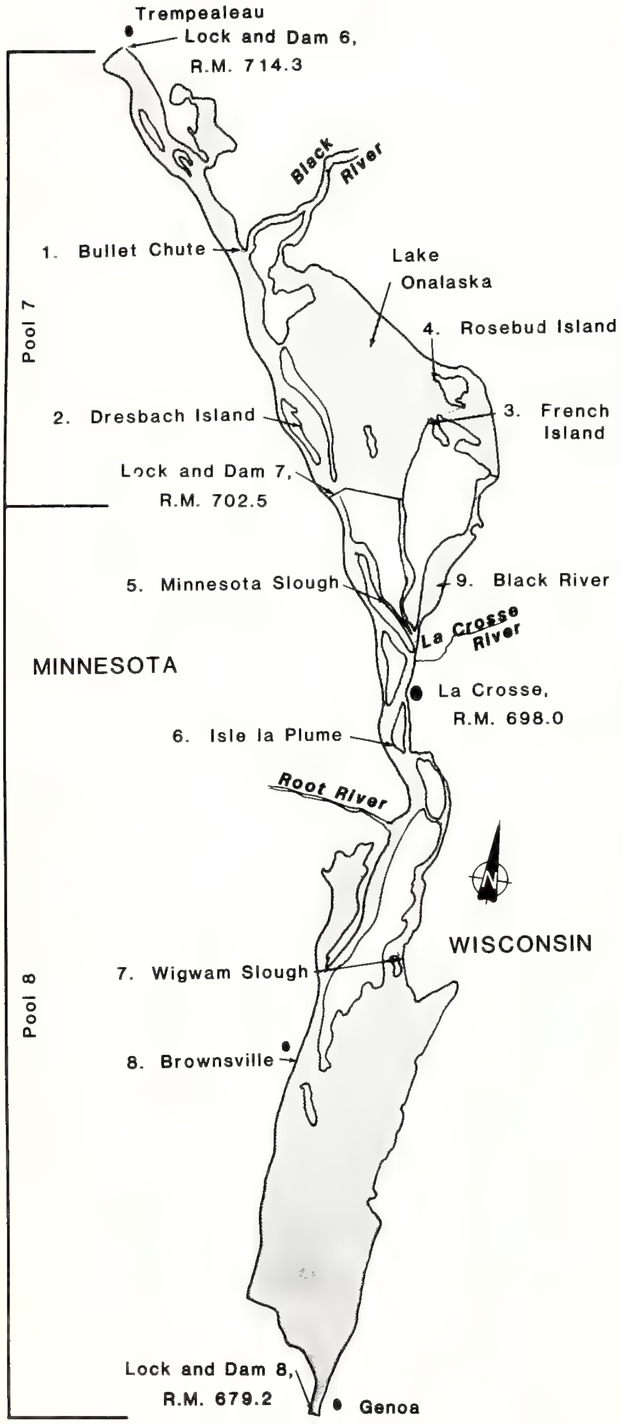

Fig. 1. Sampling sites in Mississippi River Pools 7 and 8, 1969–1981.

1. Determine diversity of naiad species (since 1969) that have lived or are now living in various areas of Pools 7 and 8, particularly in locations not studied before 1965 or examined by contemporary researchers.

2. Determine the presence or absence of the federally endangered *Lampsilis higginsi* (Lea, 1857) in these pools.

3. Compare existing records from Pools 7 and 8 with present populations, and cite possible causes for apparent changes in the species composition.

GEOGRAPHIC DESCRIPTION

This study was conducted on the Mississippi River navigation Pools 7 and 8 near La Crosse, Wisconsin, from River Mile (R. M.) 682.7 to R. M. 708.6 (Fig. 1), a 26-river mile (41.8 km) segment of the Upper Mississippi River.

Pool 7 of the Mississippi River, just north of La Crosse, Wisconsin, extends from R. M. 702.5 (Lock and Dam 7) at Dresbach, Minnesota, upstream to R. M. 714.3 (Lock and Dam 6) at Trempealeau, Wisconsin. A prominent feature of Pool 7 is Lake Onalaska, a large shallow riverine lake that makes the pool the widest area of the Upper Mississippi (about 7.4 km). The lake covers a surface area of over 2,025 ha (Jackson et al., 1981). They reported that this area supports a large sport fishery and is part of the migratory route for many waterfowl species. The Black River of Wisconsin enters the pool through several braided channels, continuing through Lake Onalaska between Rosebud Island and French Island, ultimately emptying into Pool 8 at Onalaska, Wisconsin, and continuing to La Crosse.

Pool 8 of the Mississippi River extends from R. M. 679.2 (Lock and Dam 8) at Genoa, Wisconsin upstream to R. M. 702.5 (Lock and Dam 7) at Dresbach, Minnesota. Major tributaries of Pool 8 are the Black and La Crosse Rivers of Wisconsin (R. M. 698.2) and the Root River of Minnesota (R. M. 693.8). The five mile (8.0 km) navigable portion of the old Black River Channel has its own set of river miles. The city of La Crosse is adjacent to the Mississippi from approximately R. M. 693.7 to R. M. 701. The middle portion of Pool 8 is an extensive backwater system and the lower portion of the pool is wide, shallow, and slow moving, except for the navigation channel.

METHODS

Most of the sites visited in this study prior to 1977 were hand collected, but after that date SCUBA diving and a 3 m crowfoot bar were used to supplement hand collections. The crowfoot bar, considered to be 0.7% efficient (Thiel, 1981), was generally dragged for a distance of about 170 m for each sample. At some sites all live specimens (and empty shells), except excess *Amblema p. plicata* (Say, 1817), were retained. In other instances only a few representative specimens of each species from a site were retained. A large number of specimens with soft parts were preserved in a solution of 75% ethanol, 5% glycerine, and 20% water. Some live specimens were temporarily transplanted prior to being used for studies by other researchers. The taxonomic nomenclature used in this study is taken from a December 1982 list used by The Ohio State University Museum of Zoology, Columbus, Ohio (Stansbery, 1982). Most of the species collection records are vouchered by specimens on deposit at The Ohio State University Museum of Zoology. A few specimens were placed at the Milwaukee Public Museum, Wisconsin; the Academy of Natural Sciences of Philadelphia, Pennsylvania; and at the Smithsonian Institution, Washington, DC.

RESULTS

The nine major areas sampled during this study are shown in Figure 1. The results include relative abundance and diversity, and some observations on habitat characteristics.

1. Bullet Chute, Pool 7.

In 1965, Finke (1966) recorded a live, young *L. higginsi* from just below the mouth of Bullet Chute (Mississippi R. M. 708.6), a branch of the Black River. Several recent searches of the area have not revealed this endangered species, but a rare, live *Pleurobema sintoxia* (Rafinesque, 1820) was collected by SCUBA diving just north of the mouth of Bullet Chute. This species was not considered to be a regular part of the 1930 Ellis fauna (van der Schalie and van der Schalie, 1950). (Two 5-year old fresh-dead *P. sintoxia* were found on the Minnesota shoreline just west of Bullet Chute in 1982). Twelve other species were found living and two additional species were represented by empty shells, a total of 15 species. Since the Mississippi River appears to be in fair condition in Pool 7 (Jackson et al., 1981), and substratum conditions are similar to areas where *L. higginsi* is known to survive, possibly this rare species also still survives in the area.

2. Dresbach Island, Pool 7.

Finke (1966) found a live *L. higginsi* near R. M. 704 in the former main navigation channel of the Mississippi, just east of Dresbach Island. Searches in a number of areas within this channel by SCUBA diving and sampling with a crowfoot bar have not revealed this species here since 1966. The channel has some deep holes (7 m) along the riprapped banks of the series of islands between the channel and Lake Onalaska. These rocky areas serve as productive naiad habitat. The middle of the channel was characterized by a predominately sand substratum that supported moderate numbers of juvenile and adult naiades; of note were the brightly rayed and polished *Lampsilis ventricosa* (Barnes, 1823). Four live *Lasmigona complanata* (Barnes, 1823) represented the most unusual species in the area. Living individuals of 15 species and the empty shells of six additional species were found for a total of 21 naiad species in the channel east of Dresbach Island.

3. French Island, Lake Onalaska, Pool 7.

The northwest tip of French Island has been searched a number of times since 1969. This shallow (1 m) sandy area has a variety of naiades, but the fauna is always dominated by *A. p. plicata. Lampsilis ventricosa* is abundant and the *Anodonta grandis* Say, 1829, complex is common. (See Starrett, 1971, for a discussion of the latter complex.) A large number of empty *A. imbecillis* and *Toxolasma parvus* (Barnes, 1823) wash up on the shoreline after storms. (The latter species was not considered a regular part of the 1930 Ellis fauna.) Many gastropod and sphaeriid species may be found in the same manner. One live rare *Tritogonia verrucosa* (Rafinesque, 1820) has been found, making a total of 18 living species. [*T. verrucosa* is considered uncommon in the Upper Mississippi River (Fuller 1978, 1980a, 1980b; Mathiak, 1979; Thiel, 1981; Ecological Analysts, Inc. 1981).]

4. Rosebud Island, Lake Onalaska, Pool 7.

Rosebud Island is about 1.5 km north of French Island. From mid-September to the end of October, 1977, live naiades were hand collected, from an area approximately 0.8 km long on the northwest tip of the island, R. M. 706.0, under contract with the St. Paul District, U.S. Army Corps of Engineers, St. Paul, Minnesota. Specimens were obtained in 0.3 m to 1.3 m of water, 5 m to 70 m off shore. There was an abundance of submerged aquatic vegetation at this site. The substratum was mostly firm sand with some gravel near the shore; other areas were a firm to soft silt and mud. *Lampsilis radiata luteola* (Lamarck, 1819) was generally buried vertically to almost its full length, but occasionally specimens of other species were found laying on the surface of the substrate.

Nearly 600 *L. ventricosa,* 253 *L. r. luteola,* and 130 *Fusconaia flava* (Rafinesque, 1820) were temporarily stored alive (up to 8 weeks) in wire cages submerged 16 cm in the substratum near the north shore of Lake Onalaska until they were needed for silt and sand bioassay studies conducted at the National Fishery Research Laboratory (Marking and Bills, 1980). Of interest were the results of this short-term transplantation project. Mortality rate in the holding cages was extremely low, about 1%. *Lampsilis* specimens burrowed into the substratum more readily than *F. flava.* Naiades used for bioassay studies had a mortality rate of 0.4% after a 48-hour acclimation period, prior to the bioassay studies, at the National Fishery Research Laboratory.

Amblema p. plicata was about three times as abundant as *L. ventricosa,* the second most common species found at this site. Several specimens of *A. p. plicata* were found with very weak or no "ridges". *Anodonta imbecillis* was often found in mud accumulated inside of empty shells of other species. Over 2,500 living naiad specimens (17 species) were examined. *Tritogonia verrucosa* (one) was the least common species found, although only single specimens were found of several other generally more common species.

5. Minnesota Slough—Railroad Bridge, Pool 8.

Observations while SCUBA diving below the railroad bridge (R. M. 699.8) in Minnesota Slough, just east of the main channel, revealed a seemingly suitable naiad habitat. Surprisingly, there was poor naiad species diversity in depths

Table 1. Presence or numbers of naiad mollusks collected from Upper Mississippi River Pools 7 and 8 near La Crosse, Wisconsin.

	Pool 7, 1969–1981 Havlik					Pool 7					Pool 7–9	Pool 8, 1969–1981, Havlik						Pool 8			
	Bullet Chute 1980–1981	Dresbach Is. 1975–1981	French Is. 1969–	Rosebud Is. 1977, 1981	POOL 7 TOTAL	Finke — 1965	Thiel — 1981	Fuller — 1980	Mathiak — 1979	Bartsch — 1907	Ellis — 1930	Minnesota Sl. 1980–1981	Is. la Plume 1977	Wigwam Sl. 1981–	Brownsville 1977–1980	Black River 1978, 1981	POOL 8 TOTAL	Bartsch — 1907	Thiel — 1981	Fuller — 1980	Mathiak — 1979
+ 1. *Anodonta imbecillis* Say, 1829	2	2	A	7	A						10			D	D	2	A			1	A
# 2. *Anodonta suborbiculata* Say, 1831													2				A				
3. *Anodonta grandis* f. *grandis* Say, 1829			A	A	A			2	A								R	X		21	A
4. *Anodonta grandis* f. *corpulenta* Cooper, 1834	10	1	A	34	A	3	3				22	2	1	2	3	29	A	X	5		
5. *Strophitus undulatus undulatus* (Say, 1817)		D			D					X	38		D				D	X			
6. *Alasmidonta marginata* Say, 1818					R					X			D				D				
7. *Arcidens confragosus* (Say, 1829)		D			D					X	2		D				D	X		1	
8. *Lasmigona complanata* (Barnes, 1823)	4	2			A			1		X	8	D	D	1		1	A	X			
9. *Lasmigona costata* (Rafinesque, 1820)					R					X			D				D	X			
10. *Magnonaias nervosa* (Rafinesque, 1820)					R		D				5	1		2	1		A	X			
11. *Tritogonia verrucosa* (Rafinesque, 1820)		D	1	1	A		D			X	16		D	D		1	A	X	D		
12. *Quadrula quadrula* (Rafinesque, 1820)					R	1	A					1	D	3	2	100	A	X	3	49	A
13. *Quadrula metanevra* (Rafinesque, 1820)		D			D	3	D			X	1		D	D			D	X	D	1	
14. *Quadrula nodulata* (Rafinesque, 1820)					R						1						R	X	D	5	
15. *Quadrula pustulosa pustulosa* (Lea, 1831)	16	23	A	14	A	81	68	44	A	X	11	8	2	4	4	31	A	X	18	82	
16. *Amblema plicata plicata* (Say, 1817)	19	20	A	1500	A	245	287	42	A	X	24	60	1	100	1	1683	A	X	138	190	A
17. *Fusconaia ebena* (Lea, 1831)		D			D					X	2	D	D	D		D	D	X	D		
18. *Fusconaia flava* (Rafinesque, 1820)	3	3	A	130	A	35	40	8	A	X	21	8	1	2	2	59	A	X	16	65	

19. *Cyclonaias tuberculata* (Rafinesque, 1820)					R					X							R	X	D		
20. *Plethobasus cyphyus* (Rafinesque, 1820)					R					X			D				D	X			
21. *Pleurobema sintoxia* (Rafinesque, 1820)	1				A		D			X			D			D	D	X	D		
# 22. *Pleurobema rubrum* (Rafinesque, 1820)																D	D				
23. *Elliptio crassidens crassidens* (Lamarck, 1819)		D			D											D	D	X			
24. *Elliptio dilatata* (Rafinesque, 1820)			1	1	A		2			X	24		D			D	D	X	D		
25. *Obliquaria reflexa* Rafinesque, 1820	6	8	A	1	A	6	5	6		X	23	5	2	4	1	119	A	X	1	30	A
26. *Actinonaias ligamentina carinata* (Barnes, 1823)					R					X	32		D			D	D	X	D		
27. *Ellipsaria lineolata* (Rafinesque, 1820)					R	2	1			X	6			D		D	D	X	A		
28. *Obovaria olivaria* (Rafinesque, 1820)	4	11			A	21	14	22		X	6	2	17		2	D	A	X	36	22	
29. *Truncilla truncata* Rafinesque, 1820			A	1	A	1	10	2		X	8		D	6	1	24	A	X	4	9	
30. *Truncilla donaciformis* (Lea, 1827)	11	7	A	1	A		9	41			4	2	394	2	14	60	A	X	3	51	
31. *Leptodea fragilis* (Rafinesque, 1820)	D	1	A	12	A		A		A	X	20	2	9	D	6	16	A	X	A	27	A
32. *Potamilus alatus* (Say, 1817)	2	2	A	27	A	1	1	1	A	X	49	2		3	3	35	A	X	1	15	
# 33. *Potamilus ohiensis* (Rafinesque, 1820)	D	4	D	1	A			3				11	12	1	9	2	A		2	1	
# 34. *Toxolasma parvus* (Barnes, 1823)		11	D	1	A			2				1	3	2	D	1	A			162	A
35. *Ligumia recta* (Lamarck, 1819)	6	2	1	1	A	2	2	1		X	2		D	4		1	A	X	3		
36. *Lampsilis teres* f. *teres* (Rafinesque, 1820)					R					X	4		D				D	X		5	
37. *Lampsilis teres* f. *anodontoides* (Lea, 1831)					R						14		D				D	X			
38. *Lampsilis radiata luteola* (Lamarck, 1819)			A	253	A						38	D	D	10		2	A	X		4	A
39. *Lampsilis higginsi* (Lea, 1857)					R	2				X	2				1	D	A	X			
40. *Lampsilis ventricosa* (Barnes, 1823)	8	5	A	577	A	1	8		A	X	29	1	7	4	1	25	A	X	9	16	
TOTAL SPECIES	15	21	18	18	38	14	19	13	7	26	28	17	30	22	17	27	40	34	23	20	8

A = Collected alive, quantity unknown
D = Collected shell only
X = Recorded by Bartsch, 1907, U.S. National Museum, Smithsonian Institution
R = Recorded in each Pool by other researchers

All collected by Bartsch 1907 (USNM) except:
+ = Ellis 1930 (van der Schalie and van der Schalie, 1950)
# = Havlik 1969–1981

Table 1. Presence or numbers of naiad mollusks collected from Upper Mississippi River Pools 7 and 8 near La Crosse, Wisconsin.

	Pool 7, 1969–1981 Havlik					Pool 7					Pool 7–9	Pool 8, 1969–1981, Havlik						Pool 8			
	Bullet Chute 1980–1981	Dresbach Is. 1975–1981	French Is. 1969–	Rosebud Is. 1977, 1981	POOL 7 TOTAL	Finke — 1965	Thiel — 1981	Fuller — 1980	Mathiak — 1979	Bartsch — 1907	Ellis — 1930	Minnesota Sl. 1980–1981	Is. la Plume 1977	Wigwam Sl. 1981–	Brownsville 1977–1980	Black River 1978, 1981	POOL 8 TOTAL	Bartsch — 1907	Thiel — 1981	Fuller — 1980	Mathiak — 1979
+ 1. *Anodonta imbecillis* Say, 1829	2	2	A	7	A						10			D	D	2	A			1	A
# 2. *Anodonta suborbiculata* Say, 1831													2				A				
3. *Anodonta grandis* f. *grandis* Say, 1829			A	A	A			2	A								R	X		21	A
4. *Anodonta grandis* f. *corpulenta* Cooper, 1834	10	1	A	34	A	3	3				22	2	1	2	3	29	A	X	5		
5. *Strophitus undulatus undulatus* (Say, 1817)		D			D					X	38		D				D	X			
6 *Alasmidonta marginata* Say, 1818					R					X			D				D				
7. *Arcidens confragosus* (Say, 1829)		D			D					X	2		D				D	X		1	
8. *Lasmigona complanata* (Barnes, 1823)	4	2			A			1		X	8	D	D	1		1	A	X			
9. *Lasmigona costata* (Rafinesque, 1820)					R					X			D				D	X			
10. *Magnonaias nervosa* (Rafinesque, 1820)					R		D				5	1		2	1		A	X			
11. *Tritogonia verrucosa* (Rafinesque, 1820)		D	1	1	A		D			X	16		D	D		1	A	X	D		
12. *Quadrula quadrula* (Rafinesque, 1820)					R	1	A					1	D	3	2	100	A	X	3	49	A
13. *Quadrula metanevra* (Rafinesque, 1820)		D			D	3	D			X	1		D	D			D	X	D	1	
14. *Quadrula nodulata* (Rafinesque, 1820)					R						1						R	X	D	5	
15. *Quadrula pustulosa pustulosa* (Lea, 1831)	16	23	A	14	A	81	68	44	A	X	11	8	2	4	4	31	A	X	18	82	
16. *Amblema plicata plicata* (Say, 1817)	19	20	A	1500	A	245	287	42	A	X	24	60	1	100	1	1683	A	X	138	190	A
17. *Fusconaia ebena* (Lea, 1831)		D			D					X	2	D	D	D		D	D	X	D		
18. *Fusconaia flava* (Rafinesque, 1820)	3	3	A	130	A	35	40	8	A	X	21	8	1	2	2	59	A	X	16	65	
19. *Cyclonaias tuberculata* (Rafinesque, 1820)					R					X							R	X	D		
20. *Plethobasus cyphyus* (Rafinesque, 1820)					R					X			D				D	X			
21. *Pleurobema sintoxia* (Rafinesque, 1820)	1				A		D			X			D			D	D	X	D		
# 22. *Pleurobema rubrum* (Rafinesque, 1820)																D	D				
23. *Elliptio crassidens crassidens* (Lamarck, 1819)		D			D											D	D	X			
24. *Elliptio dilatata* (Rafinesque, 1820)			1	1	A		2			X	24		D			D	D	X	D		
25. *Obliquaria reflexa* Rafinesque, 1820	6	8	A	1	A	6	5	6		X	23	5	2	4	1	119	A	X	1	30	A
26. *Actinonaias ligamentina carinata* (Barnes, 1823)					R					X	32		D			D	D	X	D		
27. *Ellipsaria lineolata* (Rafinesque, 1820)					R	2	1			X	6			D		D	D	X	A		
28. *Obovaria olivaria* (Rafinesque, 1820)	4	11			A	21	14	22		X	6	2	17		2	D	A	X	36	22	
29. *Truncilla truncata* Rafinesque, 1820			A	1	A	1	10	2		X	8		D	6	1	24	A	X	4	9	
30. *Truncilla donaciformis* (Lea, 1827)	11	7	A	1	A		9	41			4	2	394	2	14	60	A	X	3	51	
31. *Leptodea fragilis* (Rafinesque, 1820)	D	1	A	12	A		A		A	X	20	2	9	D	6	16	A	X	A	27	A
32. *Potamilus alatus* (Say, 1817)	2	2	A	27	A	1	1	1	A	X	49	2		3	3	35	A	X	1	15	
# 33. *Potamilus ohiensis* (Rafinesque, 1820)	D	4	D	1	A			3				11	12	1	9	2	A		2	1	
# 34. *Toxolasma parvus* (Barnes, 1823)		11	D	1	A			2				1	3	2	D	1	A			162	A
35. *Ligumia recta* (Lamarck, 1819)	6	2	1	1	A	2	2	1		X	2		D	4		1	A	X	3		
36. *Lampsilis teres* f. *teres* (Rafinesque, 1820)					R					X	4		D				D	X		5	
37. *Lampsilis teres* f. *anodontoides* (Lea, 1831)					R						14		D				D	X			
38. *Lampsilis radiata luteola* (Lamarck, 1819)			A	253	A						38	D	D	10		2	A	X		4	A
39. *Lampsilis higginsi* (Lea, 1857)					R	2				X	2				1	D	A	X			
40. *Lampsilis ventricosa* (Barnes, 1823)	8	5	A	577	A	1	8		A	X	29	1	7	4	1	25	A	X	9	16	
TOTAL SPECIES	15	21	18	18	38	14	19	13	7	26	28	17	30	22	17	27	40	34	23	20	8

A = Collected alive, quantity unknown
D = Collected shell only
X = Recorded by Bartsch, 1907, U.S. National Museum, Smithsonian Institution
R = Recorded in each Pool by other researchers

All collected by Bartsch 1907 (USNM) except:
+ = Ellis 1930 (van der Schalie and van der Schalie, 1950)
# = Havlik 1969–1981

to 7 m. Eight species were found alive and five others were represented only by empty shells. Live specimens were generally grouped together when on rock-gravel substratum. The most unusual find was one live adult *Magnonaias nervosa* (Rafinesque, 1820), but the fauna was dominated by *A. p. plicata*.

At the comparable railroad bridge site just to the west in the main channel, hand collecting yielded nine live species and six species represented by empty shells. A number of live juveniles, including 11 *Potamilus ohiensis* (Rafinesque, 1820), were found on a shallow sand-mud flat just upstream of the bridge. Fourteen live species and three species represented by empty shells, a total of 17 species, were found at these two railroad bridge sites.

6. Isle la Plume, Pool 8.

A pre-dredging survey was conducted in 1977 for the City of La Crosse to determine the presence or absence of endangered naiades in the Mississippi River area adjacent to Isle la Plume (R. M. 695.7 to 696.1). The area above and below the site had been dredged extensively for fill in the previous 5 to 10 years. Only 11 species were found alive. Most of the 468 live specimens ranged from 2 mm to 15 mm in length. Ten species were found in small numbers, but the eleventh species, *Truncilla donaciformis* (Lea, 1827), was represented by 394 specimens and occurred at 52 of 65 sites surveyed with the crowfoot bar throughout the length and width of the area. Perhaps *T. donaciformis* is one of the first species to repopulate an area after it has been disturbed. Two species were frequently caught on the crowfoot hooks by their byssal threads: *T. donaciformis* had a clear byssus up to 15 cm long, and *P. ohiensis* had a black byssus up to 30 cm long. Only one live *A. p. plicata* was taken, and no endangered species were found on the predominantly sand substratum.

A search of the material dredged from the Upper Mississippi River near Isle la Plume revealed shells of an additional 16 species, although there was a paucity of specimens on the 45,000 cu m fill site. A total of 26 species were found in the dredged material. Most of these specimens were sub-fossil, indicating naiad species that formerly lived in the area. The subfossil *Alasmidonta marginata* Say, 1818, found here was not considered a regular part of the 1930 Ellis fauna (van der Schalie and van der Schalie, 1950). Twenty-seven species were found in the Isle la Plume area, but the present living naiad fauna appears to have declined by 59%.

A survey was also conducted in the nearby Bluff Slough by Havlik (1980a, 1981). Additional species records from the Bluff Slough site, including live *Anodonta suborbiculata* Say, 1831, and empty specimens of *L. complanata* and *L. r. luteola,* are included in Table 1. The Bluff Slough collection raises the total species found in the area to 30.

The results of the Isle la Plume survey indicated a number of changes in the distribution of naiades in the Mississippi River from that reported by Baker in 1928. Contrary to Baker's general observations, this survey revealed live naiades farther than 26 m from shore. Indeed, they were found throughout the entire 275 m width of the channel. Baker also stated that records of mollusks in water more than 7.6 m should be viewed with suspicion. In this survey the greatest concentration of adult specimens, mainly *Obovaria olivaria* (Rafinesque, 1820), was found in water nearly 9.2 m deep near the Minnesota shore.

7. Wigwam Slough, Pool 8.

Wigwam Slough, R. M. 691.2, in the backwaters of Pool 8, is an area characterized by a sand-gravel substratum, a strong current, and depths up to 3 m. Random sampling with SCUBA gear in March, 1981, revealed fairly diverse naiad populations with living individuals of 16 species and the empty shells of six additional species. A large number of *T. verrucosa* were found dead *in situ*. This seemed to suggest that siltation had not caused the demise of these specimens, but rather that non-point pollution had perhaps been responsible for this drastic decline of this species in Wigwam Slough. Two *M. nervosa* were found alive at this site. Additional survey work with a crowfoot bar did not add to the species recorded at this site.

In July, 1981, 60 live *T. verrucosa* from the Wisconsin River, Richland County, Wisconsin, marked on both valves with orange spray paint, were experimentally transplanted into Wigwam Slough about 15 m from shore in about 3 m of water. Prior to the transplant the site was marked with 4 large pieces of concrete placed on the substratum. As of November, 1981, these naiades appeared to have positioned themselves naturally in the substratum and no recently deceased specimens were found. However, in August, 1982, six of these specimens were dead, a 10% mortality rate. At least 5 to 10 years will be needed before researchers can determine if these specimens will reproduce and help reestablish the *T. verrucosa* population in Wigwam Slough.

8. Brownsville, Minnesota, Pool 8.

Searches of a number of sites in the Brownsville, Minnesota, R. M. 688.5, area yielded living individuals of 15 species and the empty shells of two additional species. In August, 1977, a stressed living specimen taken from a fresh dredge material site was presented to me for identification by Terry Bills, Brownsville. This juvenile specimen represented the smallest live *L. higginsi* (22 mm) seen from the Mississippi River. [Since that time a live specimen, 19 mm in length, has been collected near Prairie du Chien, Wisconsin, above the mouth of the Wisconsin River, Mississippi R. M. 630.8, that may be *L. higginsi* (Stansbery, 1982 personal communication).] The Brownsville specimen still represents the present-day northern-most record of the endangered *L. higginsi* living in the main stem of the Mississippi River. More complete information on the dredging at Brownsville is provided in Whiting (1982).

One live *M. nervosa* was found in the Brownsville area in 1978, representing the first live specimen of the species above Lock and Dam 8 since 1931 (Finke, 1966; Mathiak, 1979; Fuller, 1980a; Thiel, 1981).

A number of naiad shells were found near Brownsville in a shallow area just east of the main channel that also contained a number of muskrat houses. Below Brownsville, at the entrance to Venover Slough (R. M. 687.7), a large number of young naiades were found on a mud flat that was exposed during low water. Nine live *P. ohiensis* were found buried in packed sand just off shore (one to two m) at the Brownsville swimming beach, R. M. 689.1.

9. Black River Mile 1.7, Clinton Street Bridge, Pool 8. An intensive survey was conducted in 1978 above and below the Clinton Street Bridge at La Crosse for the Wisconsin Department of Transportation to determine the presence or absence of the endangered *L. higginsi* prior to the construction of a new bridge. The survey was accomplished by first conducting 49 crowfoot runs followed by SCUBA exploration of 16 potential and existing pier sites. A maximum of sixteen species (382 specimens) was recovered at one potential pier site (an area approximately 1.5 m wide and 7.6 m long).

A total of 2,197 living specimens (17 species) were found in the predominantly clay substratum. (Clay is rare in river bottoms in the La Crosse area.) *Amblema p. plicata* represented 75% of the live specimens recovered and clearly dominated the fauna. *Obliquaria reflexa* Rafinesque, 1820, and *Quadrula quadrula* (Rafinesque, 1820), the next most common species, were well represented by 119 and 110 specimens respectively, but they comprised only 5% and 4% respectively of all specimens recovered. Many juveniles of a number of species were found. Two sub-fossil *L. higginsi* were ultimately recovered from this site.

One live *T. verrucosa* represented the least comon species found. Seven species, represented by empty valves, were found by diving and increased the total species collected at the Clinton Street bridge site in 1978 to 24. Only one live specimen of *L. r. luteola* was collected even though 253 live specimens were collected several miles upstream in the Black River Channel as it flows through Lake Onalaska, Pool 7 (Site 4). A repeat dive at the bridge site in 1980 yielded another live *L. r. luteola*. This female specimen represented one of the largest specimens of the species ever deposited at The Ohio State University Museum of Zoology (150 mm long, 74 mm high, and 84 mm wide). A sub-fossil *Pleurobema rubrum* (Rafinesque, 1820), a new record for the La Crosse area, was found at the same time.

Several additional sites were investigated near Black River R. M. 5 in 1980. Live *L. complanata* and empty specimens of *Elliptio c. crassidens* (Lamarck, 1819) and *Elliptio dilatata* (Rafinesque, 1820) were found along with the usual dominance of *A. p. plicata*. This makes a total of 18 living species, with empty shells of nine additional species from the lower Black River. Since Bartsch found only 20 species in 1907 and Thiel (1981) duplicated seven of the Bartsch records (six living species and one species represented by empty shells), the 27 species found in this study represent the largest number ever recorded from the lower Black River.

Since the mid-1960's *Amblema p. plicata* has been commercially harvested intermittently from the Pool 8 segment of the Black River for the Japanese cultured pearl industry.

DISCUSSION

From 1969 to 1981 over 7,000 naiad mollusks representing 38 species, 25 as living specimens and 13 as empty shells, have been collected in Pools 7 and 8 of the Upper Mississippi River near La Crosse, Wisconsin. Five of the 13 species represented by empty shells have been found alive by contemporary researchers (Table 1) as well as empty valves of *Cyclonaias tuberculata* (Rafinesque, 1820). In addition to the 35 species recorded prior to the 1930's I have added live *A. suborbiculata, P. ohiensis, T. parvus,* and subfossil *P. rubrum* for a total of 40 species. The present-day total of living individuals of 30 species and the empty shells of 10 additional species in the La Crosse area still duplicates and even exceeds the historic records, however the living diversity has decreased by 25%. The overall total of 40 species compares favorably with the 46 species recorded from the most diverse naiad fauna of the Mississippi River at Prairie du Chien, Wisconsin, 63 river miles (100.8 km) south of La Crosse in Pool 10 (Havlik and Stansbery, 1977; Havlik and Marking 1980; Havlik, 1981). Many species in the La Crosse area are found only in small numbers in comparison to the densities found at Prairie du Chien. The La Crosse fauna is clearly dominated by *A. p. plicata,* a commercial species that is not harvested in Pool 7 and only occasionally harvested in Pool 8.

Although living specimens have been found of several species not considered to be a regular part of the Ellis fauna, no live records of several species found by Ellis have been reported since the 1930's. Several species appear to be nearly extirpated from the La Crosse area.

The majority of this study was conducted after numbers of fresh-dead endangered *L. higginsi* were found in 1976 at Prairie du Chien, (Havlik and Stansbery, 1977). Segments conducted in 1977 (Rosebud Island) and in 1978 (Black River) revealed the presence of a diverse naiad fauna (17 species) living at each site and yet no living *L. higginsi.* An analysis of the Havlik and Stansbery (1977) species assemblage revealed that *O. olivaria* was one of the species living at Prairie du Chien and yet not found at the Rosebud Island or Black River sites. Further comparisons with data from Fuller (1978) confirmed that *O. olivaria* was also present at the *L. higginsi* site in the St. Croix River near Hudson, Wisconsin. After the 1978 discovery of living *M. nervosa* near Brownsville, Minnesota, a similar comparison of the fauna from all sites known to have living *L. higginsi* again revealed that *M. nervosa* generally lived in the same areas as *L. higginsi.* Since that time living *L. higginsi* apparently have not been found at any site in the Upper Mississippi, St. Croix or Wisconsin Rivers that did not also have either *O. olivaria* or *M. nervosa* (or both species) living at the same site (an area 2.25 sq m to 510 sq m) or in close proximity (within 0.4 km)

(Fuller, 1978, 1980a; Mathiak, 1979; Perry, 1979; Ecological Analysts, Inc., 1981; Thiel, 1981, personal communication).

Since *L. higginsi* is generally associated with populations of *O. olivaria* and/or *M. nervosa,* they apparently have similar habitat requirements. Historically they are all found in big river systems and are considered deep water species (Baker, 1928; Fuller, 1978, 1980a, 1980b). Since substrata in Pools 7 and 8 are often similar to those in the Prairie du Chien area where *L. higginsi* is known to survive, I suspect that water quality, biological characteristics or other factors are important for survival and reproduction. Research on water quality and on various contaminants using *O. olivaria* and M. nervosa, along with research on the more common congeneric species of *L. higginsi, L. ventricosa* and *L. r. luteola,* might provide some insights as to the habitat requirements of that endangered species. Although *O. olivaria* is found in small numbers in the Mississippi River upstream from Lock and Dam 8 (Mississippi R. M. 679.2) to the mouth of the St. Croix River (Mississippi R. M. 811.5), *M. nervosa* is almost extirpated from this same reach of the Upper Mississippi River (Fuller, 1978, 1980a, 1980b; Thiel, 1981). Likewise, there are no recent records of *L. higginsi* living in the main stem of the Mississippi River upstream of Brownsville, Minnesota to the mouth of the St. Croix River (Havlik, 1980b).

A cluster analysis of all naiad species found in Pool 10 of the Mississippi near the Prairie du Chien area (Thiel, 1982, personal communication) revealed that *O. olivaria* [as well as *Quadrula metanevra* (Rafinesque, 1820)] was more often found with *L. higginsi* than any other species, thus adding support to the above observations.

Since several other rare species such as *P. sintoxia* and *T. verrucosa* also still survive in Pools 7 and 8, the water quality in this area of the Upper Mississippi River should be maintained and even improved.

After comparing all known historical naiad mollusk records from the La Crosse area with modern species lists, it becomes apparent that the area no longer supports an overall flourishing naiad population except for a few species.

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HABITAT DISTRIBUTION OF SYMPATRIC POPULATIONS OF SELECTED LAMPSILINE SPECIES (BIVALVIA:UNIONOIDA) IN THE WACCAMAW DRAINAGE OF EASTERN NORTH AND SOUTH CAROLINA

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ABSTRACT

Lampsilis sp., *Lampsilis crocata* (Lea), and *Leptodea ochracea* (Say) occupied the same general habitat in Lake Waccamaw, Columbus County, North Carolina during 1979–1982. Average densities of living specimens per m^2 in Lake Waccamaw were: *Lampsilis* sp. = 1.6; *L. crocata* = 0.4; and *Leptodea ochracea* = 2.9. A slight gregariousness between Lampsilinae species was noted. Cause of minor density distribution pattern differences existing between species was not explained by data from correlation analyses of species density on basis of environmental habitat or sediment characteristics. Density related to dominant habitat vegetation was examined. *Lampsilis* sp. and *L. crocata* had highest densities in the deep sand lake regions and lowest densities in shallow sand and peat regions, but *Leptodea ochracea* differed by having a homogenous density throughout the lake; a homogeneity validated by Kruskal-Wallis (nonparametric) analysis. All three species were bradytictic. *Lampsilis* sp. and *Leptodea ochracea* became gravid September-December; the former possibly becoming gravid before the latter. Gravid condition ended after June of the following year in all three species.

The term sympatric defines two or more populations, the individuals of which are physically capable of encountering one another with moderately high frequency. Sympatric populations may have different breeding seasons and be ecologically segregated as long as a high potential exists for encounter between individuals of each population (Futuyma and Mayer, 1980). Purchon (1968) suggests that sympatric species are not closely related to each other having developed adequate barriers to interbreeding before coexisting with each other.

Sympatric naiad species of the same genus or closely-related genera are not uncommon (Ahlstedt, 1980; Emberton, 1980; Havlik and Marking, 1980; Sickel, 1980; Keferl, 1981). Discussion of naiad sympatric species and their ecological interrelationships is less common.

The sympatric *Elliptio* populations in Lake Waccamaw, Columbus County, North Carolina are perhaps best documented (Morrison, 1972; Davis et al., 1981). Recent unpublished survey data of Porter demonstrates that of the four species discussed by Davis et al. (1981) [*Elliptio waccamawensis* (Lea, 1863), *Elliptio cistelliformis* (Lea, 1863)[1], *Elliptio lanceolata* (Lea, 1828) ss.[2], *Elliptio folliculata* (Lea, 1838)] only *E. waccamawensis* is common in the lake and the other three species are relatively uncommon (Table 1). Because of these low densities, frequency of encounter between these species in the lake should be low.

A Lake Waccamaw sympatric relationship, probably having a greater frequency of encounter than that occurring within the *Elliptio* populations, includes the second, third, and fourth commonest naiads in the lake, all Lampsilinae. In decreasing order of density they are: *Leptodea ochracea* (Say, 1816), *Lampsilis* sp., and *Lampsilis crocata* (Lea, 1841)

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[1] Name believed to be a synonym of *Elliptio raveneli* (Conrad, 1834).

[2] Name of Lake Waccamaw form is now *Elliptio producta* (Conrad, 1836) according to Davis or *Elliptio fisheriana* (Lea, 1838) as determined by Stansbery (personal communication).

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Table 1. Lake Waccamaw naiads, their density, order of density in the lake and normality of density data.

Naiads*	Descending naiad density order #'s	Density: $\overline{X}/m^2$	Normality of density data** Skewness (t-value)	Kurtosis (t-value)
Elliptio waccamawensis	1	22.79	1.59 (12.5)	2.43 (9.6)
Elliptio fisheriana	5	0.17	9.11 (71.7)	98.75 (388.8)
Elliptio raveneli	7	0.10	9.96 (78.4)	104.65 (412.0)
Elliptio folliculata	8	0.09	5.83 (45.9)	32.04 (126.1)
Leptodea ochracea	2	2.92	1.98 (15.6)	5.78 (22.8)
Lampsilis sp.	3	1.55	3.61 (28.5)	16.87 (66.4)
Lampsilis crocata	4	0.38	5.05 (39.7)	30.63 (120.6)

*Not included are *Anodonta teres* Conrad (order #6, density = $0.14/m^2$), *Toxolasma pullus* (Conrad) (order #9, density = $0.02/m^2$), and *Villosa ogeecheensis* (Conrad) (order #10, density = $0.01/m^2$).

**t-values $> t$ 0.01, $\propto$ = 2.81 indicating non-normality.

(Table 1)[3]. This paper explores the available Lake Waccamaw data on the sympatric interrelationships between *Leptodea ochracea, Lampsilis* sp., and *Lampsilis crocata.*

MATERIALS AND METHODS

Description of Lake Waccamaw, its geographical location (Fig. 1), and methods used are discussed by Porter and Horn (1980) and Horn and Porter (1981). The lake bottom was divided into four sampling regions: "shallow sand" (< 1 m depth), "intermediate sand" (1–3 m depth), "deep sand" (> 3 m depth), and "peat." Each region was divided into subregions based on directional location from the center of the lake (regions and subregions are illustrated in Fig. 1, Horn and Porter, 1981). Attempts were made to sample regions equally and randomly. Three hundred and seventy-seven quantitative benthic samples were taken from Lake Waccamaw during 1979–1981. Figures 2–4 illustrate randomness of sampling. Additional non-quantitative samples were taken from Big Creek and Waccamaw River (Fig. 1). Physical data collected at sample sites included: depth, surface and bottom water temperatures, dissolved oxygen, light penetration, chlorophyll *a*, pH, dominant plant community, and sediment. Sediment samples were analyzed for percent organic matter and percent carbonate fraction. Graphic mean sediment size, sediment graphic standard deviation, sediment graphic skewness, and sediment graphic kurtosis were determined from each sediment sample (see Folk, 1974). Identifications of naiads follow suggestions by Stansbery (personal communication)[4] [see also Horn and Porter (1981) and Porter and Horn (1980)]. Representative specimens of each species have been accessioned into the mollusk collections of the Museum of Zoology, Ohio State University and the University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, North Carolina. Data analysis used SAS-BMDP interactive statistical programs in the University of North Carolina Computation Center. A Kruskal-Wallis (non-parametric) one way analysis of variance test was used after it was noted that much of the data was not distributed normally [see Dixon and Brown (1979) and Sokal and Rohlf (1969)].

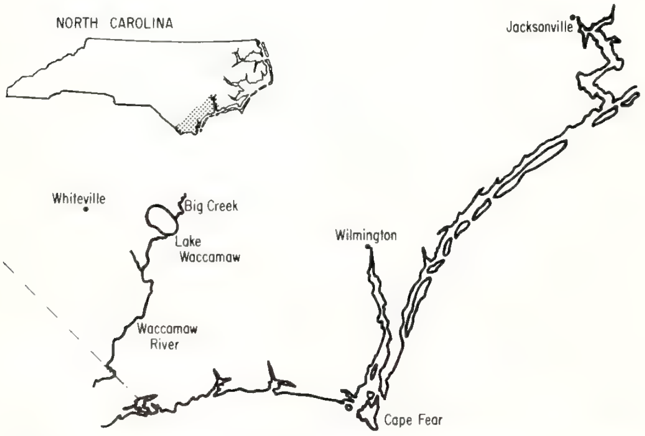

Fig. 1. Relative location of Lake Waccamaw, Big Creek and Waccamaw River in southeastern North Carolina.

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[3] Other Lampsilinae existing in Lake Waccamaw [*Toxolasma pullus* (Conrad, 1838) and *Villosa ogeecheensis* (Conrad, 1834)], part of this Lampsilinae sympatric group, are not included in this discussion because of the lack of data collected about them ($\overline{X}$ densities of each = < $0.02/m^2$).

[4] A paper describing *Lampsilis* sp. is in preparation by Stansbery.

RESULTS AND DISCUSSION

Density data and percent interrelationships between Lake Waccamaw Lampsilinae species are presented in Tables 1 and 2. Sixty percent of samples contain one or more lampsilines and 2.4% of the total samples had all three lampsilines.

The percent of samples having a lampsiline is increased if other lampsiline species are present. *Leptodea ochracea* was found in 48.7% of the total samples, yet 63.4% of the samples having *Lampsilis* sp. and 58.6% of samples having *L. crocata* contained *Leptodea ochracea* (Table 2). These percent increases are significant at the 5% level:($X^2 = 6.45$; $X^2_{0.05,\ 1} = 3.84$). Twenty-five percent of the total samples contained *Lampsilis* sp. but 34.5% of the samples with *Leptodea ochracea* and 44.8% of the samples with *L. crocata* had *Lampsilis* sp. (Table 2); percent increases are highly significant at the 1% level ($X^2 = 25.74$; $X^2_{0.01,\ 1} = 6.63$). To a slight degree a similar pattern also occurs with *L. crocata*; 8.1% of total samples had the species, but 9.4% of *Leptodea ochracea* and 14% of *Lampsilis* sp. samples had *L. crocata* (significant at 5% level: $X^2 = 4.51$; $X^2_{0.05,\ 1} = 3.84$). This increase in percent of samples containing a lampsiline suggests a gregariousness among Lake Waccamaw Lampsilinae.

Table 2. Percent frequencies of occurrence relationships between species of Lampsilinae in Lake Waccamaw*.

Species	*n* samples with species	% of total samples (372) with species	% of *n* without other Lampsilines	% of *n* with an additional Lampsiline	% of *n* with both other Lampsilines	% of *n* with *Leptodea ochracea*	% of *n* with *Lampsilis* sp.	% of *n* with *Lampsilis crocata*
Leptodea ochracea	181	48.7	63.0	32.0	5.0	XX	34.5	9.4
Lampsilis sp.	93	25.0	32.6	58.1	9.7	63.4	XX	14.0
Lampsilis crocata	29	8.1	27.6	41.4	31.0	58.6	44.8	XX

*60% of total samples contained one or more lampsiline species.
2.47% of total samples contained all three lampsiline species.

Table 3. Significant correlation summary (5 & 1% levels) for 1979–1981 Lake Waccamaw physical and molluscan density by Lampsilinae species data. Data developed from partial correlation matrix. N (=294) samples used in analyses. For physical data, only significant correlation included; 1% level indicated by "*"; $r_{0.01,\ 300} = 0.148$, $r_{0.05,\ 300} = 0.113$ *(Snedecor, 1956); high level of significance by partial correlation coefficients indicated when data is 1.5 times r* level of significance, thus significant correlation is indicated when $r_{0.01} > 0.222$ or $r_{0.05} > 0.170$ (Reish, personal communication).

Lampsilinae sp.	vs.	Species densities and physical data correlations	Partial correlation coefficients
Lampsilis sp.		*Lampsilis crocata*	0.116
		Leptodea ochracea	−0.023
		Elliptio waccamawensis	0.316*
		No physical data correlations	
Lampsilis crocata		*Lampsilis* sp.	0.116
		Leptodea ochracea	−0.008
		No physical data correlations	
Leptodea ochracea		*Lampsilis* sp.	−0.023
		Lampsilis crocata	−0.008
		Elliptio waccamawensis	0.304*
		pH	−0.194

Partial correlation analyses found no significant correlation between the lampsilines treated (Table 3). Sample density data that these analyses used was not normally distributed (Table 1, note the large numbers of samples without Lampsilinae and the high *t*-values for sample skewness and kurtosis values). Scatter diagrams comparing densities of lampsiline species against each other (not included here) provided no indication of any pattern between species.

Correlations of species density with physical habitat data and other Lake Waccamaw mollusk species densities gave results of unknown implication (Table 3). *Lampsilis* sp. and *Leptodea ochracea* populations are highly correlated with the *Elliptio waccamawensis* population (1% level). These correlations may be related to the similarity of the regional density pattern of *E. waccamawensis* which resembles the pattern of *Lampsilis* sp. (Fig. 2). Both *Lampsilis* sp. and *E. waccamawensis* are similar in that both are endemic to Lake Waccamaw; these two species and *Leptodea ochracea* are comparable as Lake Waccamaw is the only known North Carolina body of water containing major populations of all three [note Fuller (1977) comments on *Leptodea ochracea*].

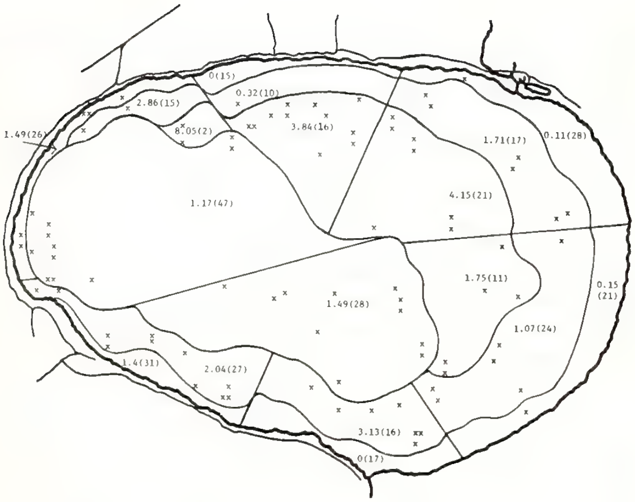

Fig. 2. Mean density, by subregion, of *Lampsilis* sp. in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *Lampsilis sp.*

Significant, but negatively correlated with *Leptodea ochracea* was pH (5% level); pH was the only measured chemical or physical parameter significantly correlated with any of the three Lake Waccamaw species of Lampsilinae. The relationship suggests that Lake Waccamaw *Leptodea ochracea* increase in density as acidity increases. Johnson (1970) recorded specimens of this species in the lower Waccamaw River, an area of probable higher acidity than Lake Waccamaw. Collections made by the senior investigator in the lower to mid Waccamaw River areas and in the lower Big Creek (Fig. 1) during 1979–1982 did not contain this species. Both of these Waccamaw drainage habitats contain mollusks but at times have pH values lower than those measured for Lake Waccamaw. Additional evidence of a tolerance by this species for pH values lower than that present in Lake Waccamaw was not found.

Mean densities of Lampsilinae species to dominant plant association are shown on Table 4. Density of *Lampsilis* sp. and *Leptodea ochracea* seem unaffected by Spatterdock [*Nuphar luteum sagittifolium* (Walt) E. O. Beal], which lines the shallow northern shores of the Lake, and Najas [*Najas quadalupensis* (Spring.) Magnus], a plant found principally in the peat substratum of the lake. Their density does seem reduced by: Maidencane (*Panicum hemitoman* Schul.), which lines the shallow southern lake shores; *Plectonema* sp., a blue-green algae; and an unidentified grass-like plant found along the lake shores. *Leptodea ochracea* density also appears adversely affected by the Maidencane and *Plectonema* beds. Density of this species increased where Spatterdock and the unknown grass-like plants occurred. No Lampsilinae or any naiads lived where a mat of *Plectonema* was present.

Table 4. Mean 1978–1981 Lampsilinae density data by dominant plant associations*, Lake Waccamaw, North Carolina. General statistics included: "N" = number of samples; "% = 0" indicates percent of samples having a zero density value. All data had high skewness and kurtosis values indicating data of a non-normal condition. Comparisons in text contrast average (mean) lampsiline "No plant" condition density vs. mean density of lampsiline species where a plant association is noted.

Lampsilinae Dominant Plant	Mean Density	Standard Deviation	Standard Error	N	% = 0	Range
Lampsilis sp.						
Unknown	2.10	3.627	0.324	125	62.4	0.0–22.6
No plants	1.70	3.949	0.346	130	76.9	0.0–22.6
Maidencane	0.17	0.734	0.121	37	94.6	0.0– 3.2
Spatterdock	1.76	3.111	0.663	22	68.2	0.0– 9.7
Najas	1.46	5.099	0.888	33	78.8	0.0–29.0
Plectonema	0.00	—	—	12	100.0	—
?Grass-like	0.00	—	—	13	100.0	—
Lampsilis crocata						
Unknown	0.59	1.980	0.177	125	88.0	0.0–12.9
No plants	0.35	1.324	0.116	130	92.3	0.0– 8.3
Maidencane	0.00	—	—	37	100.0	—
Spatterdock	0.29	1.386	0.295	22	95.5	0.0– 6.5
Najas	0.39	1.343	0.234	33	90.9	0.0– 6.5
Plectonema	0.00	—	—	12	100.0	—
?Grass-like	0.25	0.888	0.246	13	92.3	0.0– 3.2
Leptodea ochracea						
Unknown	2.78	3.448	0.308	125	48.8	0.0–16.1
No plants	3.48	4.679	0.410	130	48.5	0.0–25.8
Maidencane	1.72	2.722	0.447	37	67.6	0.0– 8.3
Spatterdock	4.58	5.854	1.248	22	40.9	0.0–19.4
Najas	2.63	3.372	0.587	33	45.5	0.0–12.9
Plectonema	0.00	—	—	12	100.0	—
? Grass-like	7.73	3.196	0.887	13	46.2	0.0– 3.7

*Plant associations:
Unknown = Dominant plant at collection site not determined.
Maidencane = *Panicum hemitomon* Schul.
Spatterdock = *Nuphar luteum sagittifolium* (Walt.) E. O. Beal.
Najas = "Water Nymph", *Najas quadalupensis* (Spreng.) Mangus.
Plectonema = Unidentified species of blue green algae.
? Grass-like = Mixture of unknown grass-like plants.

Both *Lampsilis* sp. and *Lampsilis crocata* have their greatest densities in the deep sand regions and lowest densities in shallow sand and peat regions of the lake (Figs. 2–3). This distribution is similar to that of *Elliptio waccamawensis* which has already been shown to have densities correlated with that of *Lampsilis* sp. In addition the high density area of *L. crocata* includes intermediate sand subregions.

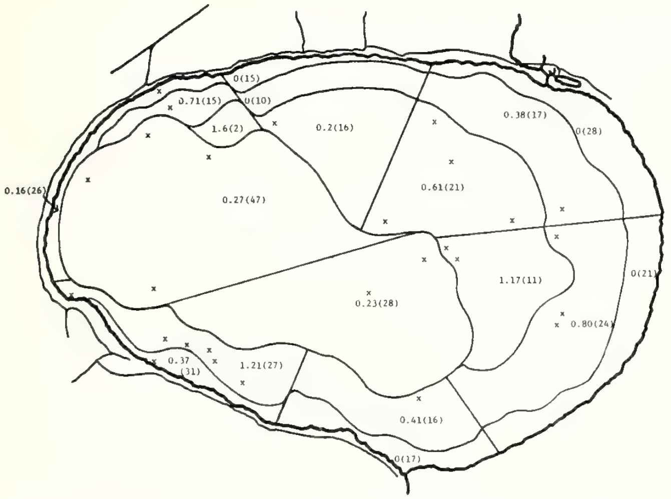

Fig. 3. Mean density, by subregion, of *Lampsilis crocata* in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *L. crocata*.

Distribution of *Leptodea ochracea* (Fig. 4) differed from that of the other two *Lampsilis* species by not having a regional or subregional pattern. This regional density homogeneity was validated by Kruskal-Wallis (nonparametric analysis of the data (Table 5). The same analysis indicated heterogeneity for the regional density data of both *Lampsilis* sp. and *L. crocata*. Physical factors affecting the species density homogeneity of Lampsilinae within the Lake Waccamaw regions or subregions have not been identified by this study.

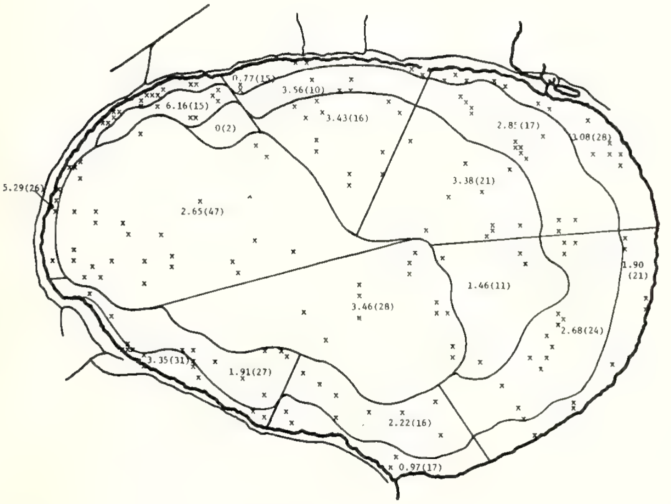

Fig. 4. Mean density, by subregion, of *Leptodea ochracea* (Say) in Lake Waccamaw. Density = specimens per m^2; ( ) = number of samples in subregion; 1978–1981 data; x = location of one or more samples containing *Leptodea ochracea*.

Table 5. Kruskal-Wallis (non-parametric) one way analysis of variance test results of 1978–1981 Lake Waccamaw ranked regional data by species of Lampsilinae. Test description in Dixon and Brown (1979) and Sokal and Rohlf (1969). Number of samples = 338. Levels of significance less than 0.01 suggest that the data is not homogenous (heterogenetic) throughout the four Lake Waccamaw regions, such values are indicated by an "*".

Variable	Kruska-Wallis Test Statistic	Level of Significance (chi-square distribution, 3 degrees freedom)
Lampsilis sp.	38.05989	0.0000*
Lampsilis crocata	15.90010	0.0012*
Leptodea ochracea	0.46155	0.9273

Species of the three Lampsilinae are known to be bradytictic. This breeding pattern was verified by the collection of gravid females of each species during winter months. Gravid *Lampsilis* sp. were collected during: September, December, March, April, and June. Gravid *Leptodea ochracea* were seen in Lake Waccamaw only in March and June. Gravid *Leptodea ochracea* were collected in Lake Waccamaw during December, February, March, April, May, and June. Ortmann (1919) listed October, November and June as months when *Leptodea ochracea* were gravid; Johnson (1970) also lists May. The period of gravid condition for *Lampsilis* sp. in Lake Waccamaw is indicated as beginning around September and ending after June of the following year. Gravid period of *L. crocata* could not be determined because not enough data was present, however the period possibly ends after June. The period of gravid condition for *Leptodea ochracea* in Lake Waccamaw may begin later than that of Lake Waccamaw *Lampsilis* sp.; first gravid *Leptodea* were not seen in September but were seen later in December. The gravid period for the species is believed to end after June of the following year. Samples of species of Lampsilinae were not large enough in any given lake area or time period to allow differences between periods of gravid condition to be judged as real or as a manifestation of interspecies variation.

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EFFECT OF A BRAZILIAN EUPHORBIACEAE ON THE PENIAL COMPLEX OF *BIOMPHALARIA GLABRATA*

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ABSTRACT

Several materials prepared from the leaves of "Canela de Urubu" *Croton sp.*, a natural plant in the northeast of Brazil, kill *Biomphalaria* spp. intermediate hosts of *Schistosoma mansoni*, at 250 to 1000 p.p.m. However, lower concentrations are not lethal to the snails, but cause relaxation of these animals and eversion of the penial complex. As is the case in the process of copulation, the preputium is everted and protrudes outside the snail. Then the anterior tip of the relaxed penis protrudes outside the preputium.

A total of 33 out of 113 (29.2%) individuals of *B. glabrata* and 2 out of 70 (3%) of *B. straminea* showed eversion of the penial complex when subjected to various concentrations of the hydrolate. The best results were obtained with 70 p.p.m. of the prepurified fraction, 50 p.p.m. of the hydrogenated, and 74 p.p.m. of the pure substance. Using extracts from "Canela de Urubu" seems to be a good method to demonstrate the detailed morphology of the penial complex of certain species of *Biomphalaria,* and to anesthetize the snails for internal surgery and physiological studies.

"Canela de urubu", *Croton* sp-09., also known as "Ervanço" (Craveiro et al., 1981) is one of the common natural plants in the northeast of Brazil. Its molluscicidal properties have been demonstrated against the snail *Biomphalaria glabrata,* intermediate host of *Schistosoma mansoni* in many parts of Brazil, (Rouquayrol et al., in preparation). It was shown in the latter studies that several materials prepared from the leaves of this plant killed snails at certain concentrations as follows: the pure hydrolate in 24 hours; the hydroalcoholic extract at 1000 ppm in 24 hours; the prepurified fraction from hydrolate at 250 and 500 ppm in 24 hours and one pure substance, geijereno isolated from the essential oil at 25, 50 and 100 ppm at 8 hours.

During the molluscicidal study another property of the plant became evident and that is lower concentrations of the hydrolate and the prepurified fraction are not lethal to the snails, in general, but cause eversion of the snail's penial complex. This property of the plant was investigated further, and the results are included in this paper.

MATERIALS AND METHODS

The plant "Canela de urubu", *Croton* sp-09 was collected from Aracati, State of Ceara, Brazil, in plastic sacs that were transported to the Department of Organic Chemistry at Federal University of Ceara (UFC) in refrigerated cars (5–10°C) to prevent evaporation. Extractions of materials from plants were carried out in the laboratory of Organic Chemistry by several procedures. 1) Hydrolate: Extractions were made with steam distillation of 3.5 kg of leaves in an extractor developed in the UFC laboratories (Craveiro et al. 1976). The mixture of vapors is condensed to a liquid state, water and essential oil are separated in different containers. The water so obtained is called a hydrolate whose constituent substances and concentration are not known. 2) Hydroalcoholic extract: Finely ground, plant material (10 g) was boiled with 50% ethanol (200 ml) with stirring for 10 minutes. The mixture was filtered, the residue discarded and the filtrate was used for tests. 3) Prepurified fraction: Extraction of the hydrolate (12 1) with ether (9 × 300 ml) afforded, after evaporation of the solvent, a residue (2 g) that was used directly for experiments with snails. 4) Pure substance: Fractionation of the above residue using column chromatography on silica gel gave a liquid substance (456 mg) with sesquiterpene skeleton and ketone function. 5) Hydrogenation: The above substance (200 mg) was hydrogenated with Pt/C 10% in acetic acid/methanol (8:2) (2 ml) in hydrogen atmosphere for 12 hours.

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The snails used in the experiments were *Biomphalaria glabrata* originally from Paulista, Pernambuco (snails 5–10 mm in diameter); *Biomphalaria straminea* from Redensao and Pentecoste, state of Ceara; *Biomphalaria tenagophila*, originally from Belo Horizonte, State of Minas Gerais and *Lymnaea (Stagnicola) elodes* from Michigan, U.S.A.

The procedures used for testing the materials were as follows:

1) Hydrolate: Dilutions of 1:1, 1:2, 1:5, 1:10 and 1:20 were made by addition of dechlorinated tap water. Observations of 2–5 snails per container were made by the naked eye and stereo microscope at 2 to 72 hours, and number of snails with everted penial complex and number of survivors were recorded.

2) Prepurified fraction GM-10 (f-56.69): One ml of absolute ethanol was added to 50 mg of the fraction to make it soluble and addition of 99 ml of water resulted in a concentration of 500 ppm. From this stock solution, other concentrations were prepared.

3) Hydrogenated: One ml of absolute ethanol was added to 20 mg of the formulation to make it soluble, and addition of 99 ml of water resulted in a concentration of 200 p.p.m. From this stock solution, other concentrations were prepared.

4) Pure substance (T.I. 7635; f-699 f-15): One ml of absolute ethanol was added to 39.5 mg of the substance to make it soluble, and addition of 99 ml of water resulted in a concentration of 395 p.p.m. From this stock solution other concentrations were prepared.

In the case of all the materials used, counts were made during 24 hours of the heart beat of *B. glabrata*.

Most of the experiments were carried out at UFC, and confirmatory tests were also conducted in New Orleans, using the same species of snails which were mailed from Fortaleza, in addition to other species.

Longitudinal serial histological sections were prepared from paraffin blocks, of the normal and of the everted penial complex. These sections were stained with hematoxylyn and eosin.

RESULTS

The effect of "Canela de Urubu" on the penial complex was more evident on *B. glabrata* than on *B. straminea* and there was no effect on *B. tenagophila*. *Lymnaea (Stagnicola) elodes*, like *B. tenagophila*, showed negative results.

The commencement of eversion varied from one snail to the other, but in some snails eversion started only two hours after contact with the hydrolate.

A total of 33 out of 113 (29.2%) of *B. glabrata* and 2 out of 70 (3%) of *B. straminea* showed eversion of the penial complex, using the hydrolate. With all concentrations of the hydrolate used there were 174 survivors out of 205 or 85% of *Biomphalaria* spp. With the prepurified fraction the best results for eversion were obtained with 70 p.p.m., with two out of five snails showing eversion. With the hydrogenated the best results were obtained with 50 p.p.m., with two out of five snails exhibiting eversion. It should be noted that at 74 p.p.m. the pure substance caused eversion of the penial complex of 71.4% of *B. glabrata*. The pure substance isolated from "Canela de Urubu" is probably a new substance, a sesquiterpene, whose final structure is under investigation in our laboratories.

In its inverted normal position the penial complex of *Biomphalaria* spp. consists of the preputium, which is a cylindrical and elongated organ and opens to the outside at the male genital opening situated near the base of the left tentacle. At the other end, the preputium continues as the vergic sac which contains the verge. The vergic sac is much smaller in diameter than the preputium. The preputium, in various species, varies in length compared to that of the vergic sac, but in *Biomphalaria glabrata* they are of almost equal length. Internally the preputium has two longitudinal muscular columns, the pilasters. Separating the cavity of the preputium from that of the vergic sac there is a muscular and secretory diaphragm consisting of several folds.

The gross morphology and histological details of the penial complex of a related species *Biomphalaria alexandrina* (= *B. boissyi*) were reported upon by Malek (1954). The internal muscular elements, and the blood (hemolymph) spaces of both preputium and the vergic sac were described and illustrated in detail. The gross morphology of the penial complex of *B. glabrata, B. straminea* and *B. tenagophila* was treated by Barbosa et al. (1968) and Paraense and Deslandes (1956).

The effect of certain concentrations of materials extracted from "Canela de Urubu" was the eversion of the penial complex of many specimens of *Biomphalaria glabrata* and a few of *B. straminea*. At the start of eversion, as is also the case in the process of copulation, the preputium is everted and protrudes outside the snail, that is, outside the male genital opening (Fig. 1). The inside layers of the preputium are now on the outside, and the outer surface of this organ is inside. The diaphragm is now at the tip of the everted preputium and its folds appear in the form of a rosette (Fig. 2).

The eversion of the preputium is followed by protrusion of the vergic sac inside the preputium. The penis is erected further, and its anterior tip shows protruding outside the preputium, usually an hour or two after eversion of the preputium. Serial longitudinal sections of the everted preputium showed the muscular pilasters on the outside, and the surface epithelium on the inside. Between the two layers there is a spaceous connective tissue region, with a few muscle fibers, and with abundant hemolymph spaces.

During relaxation of the snail, that is, with the head-foot region extending outside the shell, eversion of the preputium and erection of the penis continued for up to three days in the "Canela de Urubu" materials. When such snails were returned to water the penial complex retracted inside the animal and they returned to moving normally.

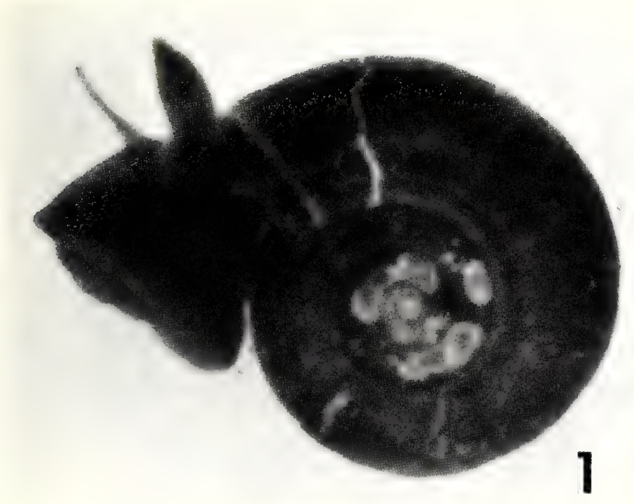

Fig. 1. *Biomphalaria glabrata* with preputium everted and protruded outside the snail next to the tentacle. Horizontal field width = 2.2 cm.

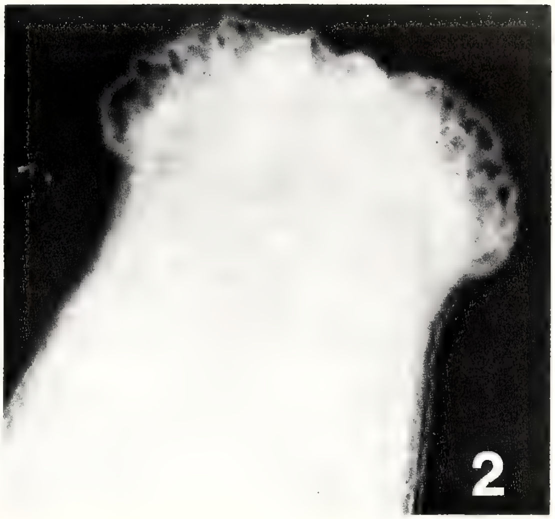

Fig. 2. Everted preputium enlarged showing folds of the diaphragm appearing in the form of a rosette. Horizontal field width = 6.0 mm.

Our observations on the effect of "Canela de Urubu" on the heart beat showed that although with some snails there was a noticeable reduction, such a phenomenon was not consistent, and it seems that more experiments and observations are necessary to clarify this matter.

DISCUSSION

The present study showed that various materials extracted from "Canela de urubu" caused relaxation of the snail, eversion of the preputium and protrusion of the penis of a large number of *Biomphalaria glabrata* and a few *B. straminea.* This condition of the penial complex normally takes place in preparation for copulation in these hermaphroditic snails. That the snails usually survived for up to three days in a relaxed condition and recovered and returned to normal when placed back in water indicates that its effect is similar to that of some substances that are used for anesthesia of snails, rather than the effect of narcotics. Its effect is, however, similar to that of some narcotics of snails such as menthol, in that it causes eversion of the penial complex. It has been our experience that when menthol is used as a narcotic to relax snails before fixation for morphological studies, the snails will have, in addition to relaxation, various degrees of eversion of the penial complex.

We can foresee several uses for "Canela de Urubu". It is a good method to demonstrate the detailed morphology of the penial complex of species of *Biomphalaria.* Further studies may prove its use as an anesthetic for internal surgery on snails, and physiological studies, for example, on the nervous system, muscles and heart. It can also be used as a tool in crossing experiments among hermaphroditic snails. This can be affected by cutting the penis after its relaxation and protrusion, and experimenting with the resulting snail as a female snail.

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UNIONID MOLLUSKS OF THE MISSOURI RIVER ON THE NEBRASKA BORDER

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ABSTRACT

The Missouri River, bordering Nebraska, has previously been reported to be uninhabitable for unionid mollusks. Studies conducted in the Missouri River and its backwaters, primarily during 1981 and 1982, revealed the presence of thirteen species and subspecies of unionid mollusks. The apparent absence of any extensive prior unionid work in the Missouri River may explain the discrepancy between this and previous literature.

Little has been written on the unionid fauna of the Missouri River in general, and almost nothing on that portion of the river bordering Nebraska. Collections were reported during the nineteenth century from the Great Falls of the Missouri River in Montana (Cooper, 1870), and at Fort Clark in North Dakota (Lea, 1858; Hayden, 1862). In Missouri, Utterback (1915–1916) collected one species in sloughs and bayous along the Missouri River, but he was insistent that no unionids occurred in the river proper. More recently, Cvancara (1975) reported an absence of unionids in the North Dakota sector of the Missouri River.

In that portion of the Missouri River contiguous to Nebraska, no previous literature is available to document the presence of unionids. Aughey (1877) does not mention the river, and there is no evidence to suggest that he collected in the Missouri River. More recent workers (Coker and Southall, 1915; Over, 1915, 1942) have described this portion of the Missouri River as devoid of unionids.

The current paper is an outgrowth of a continuing and presently unpublished study of the unionid fauna of Nebraska. Until 1976, this study had proceeded under the assumption that unionids did not inhabit the Missouri River. At that time, a questionnaire was distributed to conservation officers in Nebraska requesting information on the location of known populations of unionid mollusks in the state. Comments received in response indicated the presence of numerous populations in backwater areas of the Missouri River and suggested the need for a survey.

METHODS

The goals of this study were to document, through limited sampling, the presence of unionids in the Missouri River and adjoining and disjunct backwaters, and to gain a general understanding of the species present. The area selected for the survey extends from Santee, Nebraska to the confluence of the Platte and Missouri Rivers below Omaha (Fig. 1). The diversity of habitat in this sector of the Missouri River made it an ideal area for initial survey work. Included in the survey area are a reservoir (Lewis and Clark Lake), backwaters, oxbow lakes, and both channelized and unchannelized portions of the Missouri River.

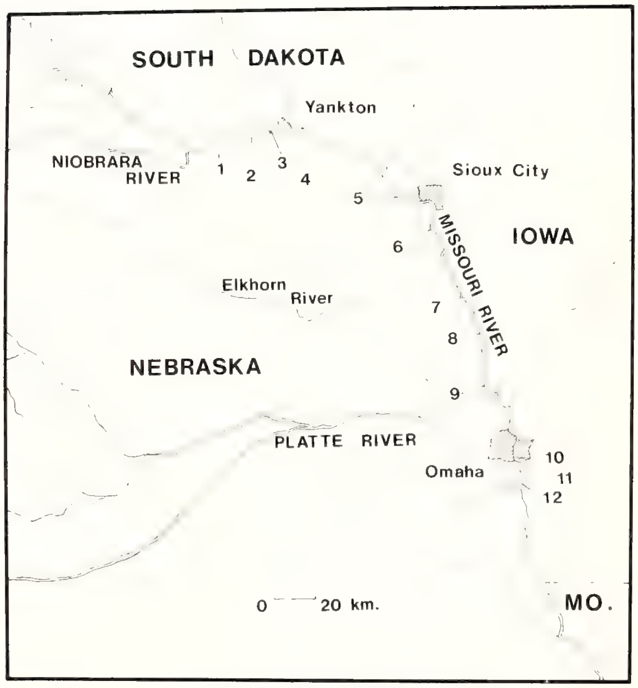

Fig. 1. Survey area and sites collected.

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Collection sites were determined primarily by accessability, and sites were sampled under low water conditions by hand or with the use of a rake. An attempt was made to obtain collections from all major habitats present in the survey region (Table 1). A number of sites were collected by area biologists. In addition, museum collections were examined for relevant specimens at the following institutions: the Ohio State University Museum of Zoology; the University of Nebraska at Omaha; and the Nebraska State Museum in Lincoln, Nebraska.

One species, *Tritogonia verrucosa* (See Table 2 for authors and dates of taxa), was identified solely by the writer. The identifications of voucher specimens of all other species recovered were corraborated by Dr. David H. Stansbery, Ohio State University Museum of Zoology, and specimens documenting this study have been deposited at that institution. The nomenclature used in this paper is that employed by Dr. Stansbery.

RESULTS

Initial survey work at ten collection sites resulted in the recovery of 11 species from the Missouri River and its backwaters. An examination of records at the Ohio State University Museum of Zoology and the University of Nebraska at Omaha resulted in the addition of one subspecies, *Anodonta*

Table 1. Collection sites.

Site	Location	Environment	Year
1	Lewis and Clark Lake, 1.3 km. east of Santee, Nebraska, Knox County, Nebraska	Backwaters of reservoir	1981
2	Lewis and Clark Lake at and above mouth of Weigand Creek, Knox County, Nebraska	Reservoir	1981
3	Missouri River, 1.0 km. east of Gavin's Point Dam, Yankton County, South Dakota	Missouri River, in current	1982
4	Missouri River, 1.3 km. above the mouth of Bow Creek, Cedar County, Nebraska	Missouri River (unchannelized)	1977
5	Missouri River mile 745.8, Dixon County, Nebraska	Missouri River (unchannelized)	1976
6	Omadi Bend, 6.4 km. NE of Homer, Nebraska, Dakota County, Nebraska	Oxbow of the Missouri River	1974
7	Missouri River, 8.8 km. ESE of Decatur, Nebraska, Burt County, Nebraska	Missouri River and backwaters	1981
8	Missouri River, 11.2 km. ENE of Tekamah, Nebraska, Burt County, Nebraska	Backwaters of the Missouri River	1981
9	Cottonwood Marina, 5.5 km. NNE of Blair, Nebraska, Washington County, Nebraska	Backwater area	1981
10	Missouri River, 1.0 km. south of U.S. 275 bridge, Pottawattamie County, Iowa	Missouri River (channelized)	1981
11	Hidden Lake, Fontenelle Forest Nature Preserve, Bellevue, Nebraska	Oxbow Lake (Dry)	1981
12	Missouri River, at Sarpy County—Cass County line	Missouri River (channelized)	1981

Table 2. Unionid mollusks collected.

Unionid Mollusks	Collection Sites												Species Frequency
	1	2	3	4	5	6	7	8	9	10	11	12	
Anodonta suborbiculata (Say, 1831)	—	—	—	—	—	D	—	F	F	—	—	—	25.0%
Anodonta grandis grandis (Say, 1829)	—	L	L	—	M	—	L	—	F	L	D	—	58.3
Anodonta grandis corpulenta Cooper, 1834	—	—	—	—	M	—	—	—	—	—	—	—	8.3
Lasmigona complanata (Barnes, 1823)	D	D	L	—	M	—	L	—	—	—	—	—	41.7
Tritogonia verrucosa (Rafinesque, 1820)	—	—	—	M	—	—	—	—	—	—	—	—	8.3
Quadrula quadrula (Rafinesque, 1820)	—	D	D	—	—	—	—	—	—	—	—	—	16.7
Truncilla truncata (Rafinesque, 1820)	—	L	L	—	—	—	—	—	—	—	—	—	16.7
Truncilla donaciformis (Lea, 1827)	—	—	D	—	—	—	—	—	—	—	—	—	8.3
Leptodea leptodon (Rafinesque, 1820)	—	—	F	—	—	—	—	—	—	—	—	—	8.3
Leptodea fragilis (Rafinesque, 1820)	—	F	L	—	M	—	F	—	—	L	—	L	50.0
Potamilus alatus (Say, 1817)	—	—	L	—	—	—	—	—	—	—	—	—	8.3
Potamilus ohiensis (Rafinesque, 1820)	D	F	L	—	M	—	L	F	F	—	—	L	66.7
Lampsilis teres teres (Rafinesque, 1820)	—	—	—	—	—	—	E	—	—	—	—	—	8.3
Number of Species Collected by Site	2	6	9	1	5	1	5	2	3	2	1	2	

L = live F = fresh dead M = museum specimen D = recent dead E = eroded dead shell *grandis corpulenta,* and one species, *T. verrucosa,* respectively to the preliminary species list obtained during the survey. All of the species recovered (Table 2) represent new published records for the Nebraska sector of the Missouri River, and at least ten represent new records for the entire Missouri River. *Anodonta g. grandis* was previously reported by Utterback (1915–1916) in sloughs and bayous of the Missouri River in Missouri, and *A. g. corpulenta* was reported for the Missouri River by Simpson (1900). *Leptodea fragilis* may have previously been collected from the Missouri River, however, the writer was unable to verify Simpson's related record as given by Utterback (1915–1916). It is anticipated that additional species will be added to the current species list as research on the Missouri River proceeds.

Although unionids were found at every site collected, the species diversity at most sites was low. Species collected per site ranged from a low of one to a maximum of nine with an average of 3.3 species per site. Collecting conditions at site 1 probably adversely affected the sampling activities at that site, while a ten foot drop in the level of the Missouri River at site 3 was partially responsible for the relatively high number of species represented in the collection from that site. Despite these potential variations, it is believed that the collections at most sites are probably representative of the local unionid fauna. The low number of species recovered from sites 10, 11, and 12 probably reflects the impact of the channelization of the Missouri River at these sites and the resultant elimination of habitat.

Potamilus ohiensis, Anodonta g. grandis and Leptodea fragilis, were the most common species found, and were collected in practically all habitats sampled. *Anodonta g. grandis* and *P. ohiensis* were most abundant in quiet backwaters of the Missouri River and in Lewis and Clark Lake, while *L. fragilis* was the most abundant species at sites 3 and 12 in the current and substrate of the Missouri River proper. *Lasmigona complanata,* while widely distributed in the survey area, was not abundant at any collection site.

The recovery of specimens of *Anodonta suborbiculata* represents the first record of this species in Nebraska in more than a century. It has previously been reported by Aughey (1877) for the Elkhorn and Blue (probably the Big Blue) Rivers, but has not been reported in the Nebraska sector of the Missouri River. *Anodonta suborbiculata* was found in relatively quiet backwaters with sand or soft mud bottoms. It was not present in backwaters that were even infrequently subjected to the strong currents of the Missouri River.

The discovery of *Leptodea leptodon* is of particular interest since this species is currently under review for possible inclusion in the U.S. List of Endangered and Threatened Wildlife and Plants. A single fresh dead specimen was found at site 3, and represents the only such specimen in almost fifteen hundred unionids examined at that site. A report of *L. leptodon* (as *Unio tenuissimus*) in the Nemaha River (Aughey, 1877) appears to be the only other published record of this species in the Missouri River Basin.

DISCUSSION

The results of this study contrast sharply with statements made in previous literature. Other workers have reported an absence of unionid mollusks from the Missouri River and have attributed this to the high silt content of the river's waters (Over, 1915, 1942; Utterback, 1915–1916, 1917; Bartsch, 1916). Though Hayden (1862) collected some unionids from the Missouri River, he also reported the river to be so turbid that living mollusks seldom occurred.

Within the past forty years, the construction of six major dams on the Upper Missouri River has resulted in a dramatic decrease in the silt content of the river's waters as silt loads have settled on the impoundment substrates. It is thus possible that the decrease in silt has enabled unionid mollusks to colonize a formerly uninhabitable environment. Any such conclusion presupposes, however, that early research was extensive enough to document their former absence from the Missouri River.

An examination of the relevant literature provides no indication of the extent of previous collection efforts on the Missouri River. In fact, there are no published statements to suggest that any determined effort has ever been made to document the status of unionids in the Missouri River. Coker and Southall (1915) did not collect in the Missouri River and dismissed it as a possible habitat for unionids. Over (1915, 1942) devoted only one sentence to the subject in each of his publications, and gave no indication of the extent of research effort involved in arriving at his conclusions. Bartsch (1916) described the Missouri River as a faunal barrier to unionids based solely upon the absence of unionids in the Mississippi River below St. Louis, Missouri and the high silt content of the Missouri River at its confluence with the Mississippi River. There is no indication that Bartsch conducted any related survey work in the Missouri River. Utterback (1915–1916, 1917) viewed the Missouri River as a faunal barrier to unionid life, but provided no indication of related collection activities.

While early statements describing the Missouri River as uninhabitable for unionids may have been correct, they do not appear to have been supported with extensive survey work. In fact, some of Utterback's collections seem to point toward the presence of unionids in the Missouri River. Of particular interest are collections of unionids from oxbow lakes of the Missouri River near St. Joseph, Missouri (Utterback, 1915–1916). The unionid fauna reported for these lakes is similar to that found during the current study, and suggests that a comparable fauna may have been present in the Missouri River and its backwaters at that time. It is possible that the high silt content of the Missouri River may have been less detrimental to unionids than has previously been assumed.

CONCLUSIONS

It is difficult to reconcile the results of the current study with statements made in previous literature. While others have reported the Missouri River to be without unionid life, results of the current study revealed the presence of thirteen species and subspecies. Though it is possible to explain this discrepancy as the product of a recent decline in the silt content of the Missouri River, the apparent absence of extensive previous work in the Missouri River may be a more probable explanation.

ACKNOWLEDGEMENTS

A number of individuals contributed their time and efforts to this project. Andy Saunders, Fontenelle Forest Nature Preserve, Bellevue, Nebraska provided the specimens collected from site 12. Bob Thomas, Nebraska Game and Parks Commission, Lincoln, Nebraska provided the collection at site 6 as well as useful information on potential collection sites. Keith Perkins, Sioux Falls College, Sioux Falls, South Dakota collected the specimens at site 5. Thanks are also due to Dr. Richard Stasiak, University of Nebraska at Omaha, for permission to utilize records from that institution relating to site 4, and to Dr. Patricia Freeman, University of Nebraska State Museum, Lincoln, Nebraska for courtesies extended during numerous visits to that facility. I am most indebted to Dr. David H. Stansbery, Ohio State Museum of Zoology, Columbus, Ohio for corraborating identifications, and for his interest and encouragement during the course of the project.

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IN MEMORIAM

WILLIAM ERWOOD OLD, JR.

April 14, 1928–December 31, 1982

William E. Old, Jr.
(photo by R. Robertson)

The death of Bill Old, in New York City on December 31, 1982, was a stunning shock to his many friends and colleagues. Bill has been described as "a natural history prodigy"— and so he was. He was born, raised and educated in Norfolk, Virginia, where his interest in natural history developed at an early age. While in his teens he did volunteer work at the Smithsonian Institution, where he was encouraged by naturalist Austin H. Clark and William M. Mann, the director of the National Zoological Park.

He attended the College of William and Mary, Norfolk Division, in 1946–47, served with the United States Army in the Korean War, and again attended William and Mary, 1954–56. Just when mollusks became his major interest we do not know, but while in his 20's he had already assembled a collection and become very knowledgeable of the phylum.

In July of 1960 Bill left a mundane job in Virginia to join the staff of the American Museum of Natural History as "Museum Specialist" in the Department of Invertebrates. Through the years he progressed to become the department's highly valued Senior Scientific Assistant, and the reference collection of mollusks nearly tripled in size during his more than two decades as the collection manager. He had a tremendous knowledge of his subject, and a phenomenal memory with instant recall. Bill was a recognized authority on the family Conidae, but he generated equal enthusiasm for other groups—including Strombidae, Cypraeidae, and the Chitons, as well as fossils and terrestrial gastropods.

Among his hobbies was a keen interest in zoological gardens. This past summer he toured 17 European zoos. He was a practicing horticulturist specializing in cactus and other succulents. His many cultural interests included literature, history and classical music.

Bill was the author or co-author of some 36 scientific papers on molluscan subjects and he contributed numerous popular articles and book reviews to shell club journals. He assisted in the preparation of several guide books on mollusks, including the *American Museum of Natural History Guide To Shells,* by Emerson and Jacobson, and the recently issued *Seashells of Oman,* by Donald and Eloise Bosch.

Bill was always ready to help the amateur. He was friendly and interested. He lectured at shell club meetings and taught adult education classes at the museum. He judged shell shows all over the country. These activities were

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in addition to his regular duties. His extensive travels included field trips to the West Indies, Galapagos Islands, Mexico, and Peru, and visits to study the collections of museums in England and Europe.

Bill was an active member of several Natural History organizations and served as president for the New York Shell Club (1963–65) and the American Malacological Union (1978–79). He was a positive influence in the field of malacology and his contributions will be long remembered.

As a memorial to Bill, the American Museum of Natural History has established the William E. Old Malacology Fund. Contributions to the Fund will be used to support the Department's malacology program, especially the collection, on which Bill worked with extreme dedication for more than twenty-two years.

Dorothy Raeihle and William K. Emerson
New York City, New York
24 January 1983

NEW MOLLUSCAN TAXA DESCRIBED BY WILLIAM E. OLD, JR.

Ximeniconus Emerson and Old, 1962 (a subgenus of *Conus*).
Lotoria Emerson and Old, 1963 (a subgenus of *Cymatium*).
Cymatium perryi Emerson and Old, 1963.
Scalptia mercadoi Old, 1968.
Haustellum wilsoni D'Attilio and Old, 1971.
Conus vicweei Old, 1973.
Scaphella contoyensis Emerson and Old, 1979.

SPECIES DESCRIBED IN HONOR OF WILLIAM E. OLD, JR.

Takydromus tachydromoides oldi Walley, 1958
Strombus oldi Emerson, 1965

SCIENTIFIC PUBLICATIONS WILLIAM E. OLD, JR.

1956 (and Roger H. Rageot) "Land snails of Nansemond, Norfolk, and Princess Anne Counties, Virginia." *Virginia Journal of Science* 7(2):87–90.

1962 (with William K. Emerson) "Results of the Puritan–American Museum of Natural History Expedition to Western Mexico. 16. The Recent mollusks: Gastropoda, Conidae." *American Museum Novitates* No. 2112, 44 pp., 20 figs.

"*Cypraea (Blasicrura) coxeni* Cox." *The Cowry* 1(4): 52–56, pls. 6, 7.

1963 "What is *Cypraea arabica niger* Roberts?" (Abstract) *American Malacological Union Annual Reports* 1962: 13.

(with William K. Emerson) "Remarks on *Cassis (Casmaria) vibexmexicana*." *Nautilus* 76(4):143–145, pl. 10.

(with William K. Emerson) "Results of the Puritan-American Museum of Natural History Expedition to Western Mexico. 17. The Recent mollusks: Gastropoda, Cypraeacea." *American Museum Novitates* No. 2136, 32 pp., 18 figs.

(with William K. Emerson) "A new subgenus and species of *Cymatium* (Mollusca, Gastropoda)." *American Museum Novitates* No. 2137, 13 pp., 6 figs.

"Cowries from the Lesser Sunda Islands." *Treubia* 26, pt. 2: 71, 72.

"*Cypraea latior* Melvill, 1888." *Hawaiian Shell News* 12(2):4, 6 figs.

(and Anthony D'Attilio) "Remarks on *Conus telatus* Reeve (Mollusca: Gastropoda)." *Veliger* 6(2):60–61, figs. 1–3.

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1965 "Comments on *Thais (Tribulus) planospira*." (Abstract) *American Malacological Union Annual Reports* 1964:47–48.

(with William K. Emerson) "New molluscan records for the Galapagos Islands." *Nautilus* 78(4):116–120.

"On the identity of *Conus pastinaca* Lamarck." *Nautilus* 79(1):23–26, 2 figs.

(with William K. Emerson) "Additional records for *Cypraea surinamensis* Perry." *Nautilus* 79(1):26–30, pl. 3.

1966 (with William K. Emerson) "*Cypraea (Propustularia) surinamensis* Perry from Brazil." *Nautilus* 80(2): 70–71.

(with William K. Emerson) "Additional records for *Strombus oldi*." *Hawaiian Shell News* 14(13):7, 1 fig.

"Comments on *Conus gloriamaris*." *Hawaiian Shell News* 14(9):4–5, 7; 6 figs.

1967 (with Morris K. Jacobson) "On the identity of *Spisula similis* (Say)." *American Malacological Union Annual Reports* 1966:30–31.

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IN MEMORIAM

KATHERINE VAN WINKLE PALMER

February 4, 1895–September 12, 1982

With the death on September 12, 1982 of Dr. Katherine Van Winkle Palmer, the American Malacological Union lost a distinguished Past President.

Dr. Katherine V. W. Palmer, nee Katherine Evangeline Hilton Van Winkle, was born February 4, 1895 in Oakville, Washington. She attended the University of Washington where she studied under Dr. Charles E. Weaver, receiving her B.S. in 1918. After graduation she went to study under Professor Gilbert D. Harris at Cornell where she was twice the Goldwin Smith Fellow in Geology. It was her intention to return to Washington and work with Dr. Weaver on the Eocene fauna of the north-west. These plans were permanently changed on December 24, 1921 when she married Dr. Ephraim Laurence Palmer, a professor at Cornell who later became well-known as a naturalist and author. She continued her studies after marriage and received her Ph.D. from Cornell in 1925, having been slowed down somewhat by the birth of her first son in 1923. A second son was born in 1930.

At Cornell Professor Harris had established his own press to publish papers written by himself and his students, and to reprint older, unavailable literature. This press evolved into the Paleontological Research Institution of which Katherine Palmer was a Founding Member. When Professor Harris died in 1951 she became Director of the P.R.I., a position she held until her retirement in 1978. The interesting history of that Institution is the subject of her last published work, *Paleontological Research Institution, Fifty Years, 1932–1982,* which was published by the P.R.I.

Katherine Palmer received world-wide recognition as a paleontologist, and in 1972 was the recipient of the prestigious Paleontological Society Medal, presented by the Paleontological Society of America. She was the first woman to receive the Medal, and the first recipient who worked with mollusks. In 1978, during a symposium held in her honor, she received an honorary Doctor of Science degree from Tulane University.

Her interest in mollusks was not confined to fossils, and she was a Life Member of the American Malacological Union, which she served as President in 1959–60. She was a regular attendee at the A.M.U. Annual Meetings where she presented several papers. In addition to her membership in the A.M.U. Katherine Palmer held memberships, either active or honorary, in numerous societies and organizations, including: Alpha Delta Pi; Sigma Xi; Phi Kappa Phi; Sigma Delta Epsilon, which she served as National President; Chi Upsilon, National Councillor; Paleontological Society of America, Fellow; Geological Society of America, Fellow; American Association for Advancement of Science, Fellow; American Association of Petroleum Geologists, Fellow; Society of Economic Paleontologists and Mineralogists; Geological Society of France, Life Member; Société Linnéenne de Lyon, Life Member; Cushman Foundation for Foraminiferal Research, Fellow.

Many of her publications dealt with Recent mollusks, but she will be most remembered by malacologists for her work on the Veneridae of the southeastern United States and for her publications on the mollusks described by P. P. Carpenter, the latter works being indispensable to anyone working on the mollusks of the Pacific coast of the Americas. She was also keenly interested in systematic nomenclature and was a participant in both the Copenhagen Colloquium on Zoological Nomenclature in 1953 and the London Colloquium of 1958. During her career she published over 70 books and papers. A complete bibliography appears immediately following her final scientific paper in *Tulane Studies in Geology and Paleontology* (1979, 15(1–4):74, 94, 104, 128) to which should be added the aforementioned history of the P.R.I. This bibliography reflects her wide range of interests in invertebrate paleontology, malacology, stratigraphy, biography, bibliography and nomenclature.

A memorial of this sort can pay only partial tribute to Katherine Palmer's capability, integrity, vitality and inspirational ability. She successfully combined being wife, mother, editor, institutional director, and publishing scientist. In a memorial to Professor Harris she wrote: "To all he was a genial, helpful companion with an every-ready sense of humor." This phrase could as easily have been written about her, as her sense of humor was a subject of note even in her student days. Katherine Palmer was never too busy with her own work to assist, not only her fellow scientists, but to lend aid, encouragement and direction to amateurs. For the last two years of her life she was unable to continue her own research due to physical disability, but her mind was unimpaired and until her final days she continued to offer advice and assistance to others.

She was held in high esteem by her professional colleagues, admired by her many friends and associates, and liked by all who knew her. To future generations of paleontologists and malacologists she will be known only by her published work, which remains as a monument to her ability and dedication as a scientist. To those of us who had the privilege of knowing her, she will always be remembered as a very exceptional and special person.

Dr. Katherine V. W. Palmer is survived by one son, Richard Robin Palmer.

Richard E. Petit
North Myrtle Beach, South Carolina
14 February 1983

THE AMERICAN MALACOLOGICAL UNION
48th ANNUAL MEETING

JULY 19–23, 1982
NEW ORLEANS, LOUISIANA, U.S.A.

LOUISE R. KRAEMER, 1982 Presidential Address to the American Malacological Union: Mollusks, the A.M.U. and the Golden Rule 83

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[1] The Second International Symposium on Molluscan Genetics will appear in its entirety in *Malacologia.*

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MOLLUSKS, THE A.M.U., AND THE GOLDEN RULE

1982 PRESIDENTIAL ADDRESS TO THE AMERICAN MALACOLOGICAL UNION

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Using biological criteria, we realize that there are two great groups of animals associated with the planet Earth: the Arthropods (pre-eminently insect species), and the Mollusks (pre-eminently gastropod species). Some years ago, I argued (Lytle, 1970) as surely others have done before, that to cling to Aristotle's once–upon–a–time useful distinction between *vertebrate* animals and *invertebrate* animals in the latter part of the 20th century is not only misleading, not only unscientific, but also harmful. I urged the eradication of the word, "invertebrate," from our language. The concept the word embodies is not only harmful to the animals whose role in the biosphere we thereby discount, but harmful to the future of ourselves and our unborn great grandchildren.

An alert child without our adult prejudice can see the folly of defining more than 90% of the known animal species on this planet in terms of something that less than 10% of the animal species **have**, a vertebral column—lumping together most animals as **in**vertebrates, Arthropods and Mollusks included, in terms of something they don't have! In my argument I noted that it would be far more equitable for human beings to divide the Animal Kingdom into Mollusks and Non-Mollusks, or into Arthropods and Non-Arthropods. I was accused at the time by some of my zoological colleagues of having uttered a "naughty" idea. Today it is gratifying to see that some modern authors devote a sentence to two to a similar thought, though the textbook covers still proclaim their book's contents as "invertebrate zoology." From my view, these authors are not nearly assertive or vehement enough to counter the effects of a 2000-year-old prejudice and ubiquitous "observer problem"; but at least they are saying **some**thing.

I speak to you now, therefore, as Non-Mollusks: (1) to invite your focus on the gloriously diverse species of our shared concern, the Mollusks; (2) to discuss with you a few aspects of the present and future role of the American Malacological Union, as the pre-eminent body in the Americas devoted to the study of mollusks; and (3) to examine with you some arguments relating both mollusks and the A.M.U. to certain large concerns of science and society.

MOLLUSKS

Since this past week has been the occasion of the 48th Annual Meeting of the American Malacological Union, held in the 51st A.M.U. year, we share the immediate experience of up-to-date data and ideas about the nature of mollusks. Of course, we have much to be humble about if we recall that Lewis Thomas (1978, p. 1460) noted,

> ". . . that we are profoundly ignorant about nature. Indeed I regard this as the major discovery of the past 100 years of biology."

Though mindful of that qualification, it is comforting to realize that all of us do have some understanding of what constitutes the nature of a mollusk.

As an undergraduate I remember being enchanted, mystified and uneasy over the fact that the Mollusca were the only animal group pedagogically approached with a diagram and discussion of "the Ancestral Mollusk." I soon realized that the Ancestral Mollusk was a hypothetical construct devised to aid students in understanding phylogenetic relationships within the bewildering variety of molluscan assemblages. As Yonge notes (Yonge and Thompson, 1976, p. 24), ". . . the gradual tracing of common structural features was a major triumph of comparative anatomy,"

More dramatically than in the study of many animal groups, the student of mollusks is confronted by diversity so overwhelming as to constitute a constant reminder of our great legacy from Charles Darwin, that it is the tendency of all populations, of all groups of organisms, to exhibit variations. Further, Darwin showed us that variations from one organism to another, one population to another, far from constituting "monsters" or "aberrations" from some specially created type, are to the contrary, the veritable **operating capital** of organismal groups, i.e. the genetic variation which makes possible their evolution, their survival with change.

In appreciating the vast richness of molluscan diversity one also learns that it represents variation on the themes of the molluscan body plan. In all of the Animal Kingdom one

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looks in vain for a structural/functional/behavioral complex more versatile than the molluscan mantle. For example in *Corbicula fluminea* (Müller), the recent Asian bivalve interloper in most of the managed waterways of the U.S., we can see the posterior mantle thickened with muscle into a deep siphonal pocket, sutured around the posterior adductor muscle and fused anterior to the branchial siphon into a reduced pedal gape (Kraemer, 1977). The particular, protective mantle features of *C. fluminea* accompany reproductive characteristics which allow it to survive well in the altered habitat of "managed" U.S. river bottoms: a monoecious habit, capacity for self-fertilization, and production of vast numbers of glochidia-sized, active young juvenile clams. In contrast, in the indigenous freshwater unionid bivalves, the two lobes of the mantle are unfused, far more open to freshwater currents (Kraemer, 1979). In dioecious unionid species such as those of the genus *Lampsilis,* the flared posterior edges of the mantle are expanded into flaps which are extensively innervated by way of special mantle ganglia, the latter being connected with the visceral ganglia and pallial nerves (Kraemer, 1969, 1979). Further, spawning of glochidial larvae is accompanied by greatly altered activity of the animal's foot, marsupial gills and siphons, in association with the rhythmic, paired pulsations of the mantle flaps (Kraemer, 1970).

In some species, such as *Lampsilis ventricosa* (Barnes), the extreme headstand of the animal, the rapid (3/sec) pulsing movements and the fishlike appearance of the mantle flaps remind the human observer of a small swimming minnow. Furthermore, it is possible to determine experimentally that this mussel species will alter its rate of mantle flap movements, increasing the rate of response to increments of light at low intensity (as observed in nature at dawn); and decreasing the rate in response to decrements of light at low intensity (as observed in nature at dusk), (Kraemer, 1970).

In other species of *Lampsilis* such as *L. radiata siliquoidea* (Barnes), the fish-like appearance of the mantle flaps is less obvious. The flap movements are less rapid, are not noticeably sensitive to light, and may continue for hours in the dark. In this species, however, the mantle flaps **are** very sensitive to slight water movements, to tactile stimuli and to jarring of the substrate. *Lampsilis reeveiana* (Lea) (formerly *L. brevicula*) and others have mantle flaps with some resemblance to those of *L. r. siliquoidea,* which are also very sensitive to water movements and jarring of the substrate.

Carunculina texasensis (Lea) is related to other unionid species that are monoecious, and the gravid *C. texasensis* does exhibit paired pulsing movements of the edges of the mantle near the branchial siphons (Kraemer, in press). In addition, at a location that corresponds to the site of the "tails" in the mantle flaps of the genus *Lampsilis, Carunculina texasensis* has a pair of conspicuous caruncles that will emerge after a pulsing sequence, and rotate, one clockwise, one counterclockwise, like a pair of twiddling thumbs (Kraemer, in press).

From my own studies of the structure, function and behavior of these freshwater bivalves, I realize that mollusks have much to teach us about what they do and how they do it; and that comparative behavioral studies in concert with studies of their neurobiology and reproductive physiology, are going to afford us splendid avenues for human comprehension. Fellow Non-Mollusks, have you not been impressed with the fact that certain mollusks, the cephalopods, manifest the biggest, most complex brains in the Animal Kingdom, except for the most highly developed of avian and mammalian brains? Have you not been impressed with the fact that mollusks exhibit a neurological twisting unique in the Animal Kingdom, as some gastropods during their ontogenetic torsion achieve 180° twist in their nervous systems? Have you not been impressed with the fact that mollusks are the most complex animals to exhibit essential headlessness, as the bivalves concentrate their largest ganglia and most of their sensors at their posteriors to provide them with a truly rear view of the world?

Perhaps it is their soft bodies that allow for remarkable neurological plasticity demonstrable even in bivalved mollusks. In bivalves neuronal cell bodies string out along their nerves and cluster as ganglia at the periphery, to become pacemakers for the pulsing mantle flaps in dioecious unionids (Kraemer, 1969 and in press). In some hermaphroditic freshwater bivalve species such as *Corbicula fluminea,* neuronal cell bodies may group at the ends of nerves as follicular ganglia within the confluence of oogenic and spermatogenic follicles, there presumably to orchestrate the events of monoecious reproduction (Kraemer, 1978 and in press).

The present level of human understanding of nervous system structure and function owes much to the exploitable mollusks: to the squids for their giant axons; to the octopuses for their complex, ablatable brains and their intelligent and tractable behavior; to *Aplysia* and *Tritonia* for their available ganglia, their large and consistently identifiable neuronal cell bodies and their associated behavioral responses. I suspect that future research on molluscan nervous systems will provide increasingly valuable insights regarding interactions between small networks of nerve cells, as well as interactions between brain and behavior, the central nervous system and behavior, and the vast sensory surface of the mollusk and its behavior.

Some years ago (cited in Sinsheimer, 1971, p. 21) Einstein commented that, "The most incomprehensible thing about the universe is that it is comprehensible." If this is another form of human hubris, it seems highly likely that the study of mollusks will continue to aid it!

THE A.M.U.

What then of this splendid, peculiar body, the American Malacological Union? What of its numbers of members who work on or with mollusks for a living or for the love of mollusks, or both? Malacology, like any science, must be an eminently social affair, with rigorous exchange, and show and tell and argument. Perhaps unlike some sciences, Malacology must be more of all of these—because we have so much to do, and because there are as yet comparatively few of us to do it. With members as variously talented as the animals we study, our society has the special value of providing diverse intellectual cross-fertilizations. About four hundred years ago, at the beginning of discussions of modern scientific method, Francis Bacon characterized the techniques that provide for human intellectual development when he asserted: "Reading maketh a full man; conference (discussion, talking) maketh a ready man; and writing maketh an exact man." A.M.U. has been well served by all those it has stimulated to develop as full, ready and exact men . . . and women.

As a society, the American Malacological Union must continue to appreciate the diversity of its members; because this is the diversity that provides A.M.U. with **its** evolutionary capital, **its** strong capacity for survival and growth with change. Permit me an analogy: a few years ago a certain young physiologist visited our campus at the University of Arkansas at Fayetteville. The preparation with which he carried out his physiological researches was the optic tectum of the frog's brain. He had run into difficulty with his experiments that produced capricious results. He finally decided to re-investigate the microarchitecture of the optic tectum; and consequently he re-did all of the old histological techniques and experiments upon which the prevailing human understanding of the tectum was based. It took him two years; but it paid off. He produced a reliable microanatomic base upon which not only he, but all of his colleagues, could build their physiological experiments. I commended his independent spirit, his commitment, and the personal sacrifice of his valuable time. He responded to my compliments by simply averring that all he had done was just to use his own "style." He went on to comment that he thought what made any scientific worker valuable was his **style**. I heartily agree. And may our very own style and elan continue to characterize the work of each of us in A.M.U.!

As an increasingly stronger, growing society, the A.M.U. will, of course, become increasingly capable of shouldering the legacy of voluminous molluscan concerns which the workers of the past fifty years have delineated for us. Part of this legacy which I should like to receive more attention in the future than it has in recent years includes a continuing concern with historical perspective. Such a vigorous, continuing concern will not only be immeasurably helpful to us in maintaining our scientific literacy—it will also help us to avoid, in many instances, "re-inventing the wheel." There is another part of this legacy that has been receiving strong, concerned attention from some members of A.M.U., but which in my opinion needs much more substantial, continuing and integrated support. This is a focus not only on conservation and on systematics of mollusks, but on the inevitable, practical, burgeoning connections between strong mollusk conservation policy and good communicable work on molluscan systematics.

To strengthen the legacy of the past fifty years, we have begun to develop plans for establishing a firm financial base for A.M.U. This is a new development, one which has gathered momentum within the past few years, and has led a number of us to realize that it is vital to the successful future of A.M.U. As President of A.M.U., I have been greatly concerned to realize that we operate, financially, without any substantive capital funds. Thus I, like my recent predecessors in this office, have spent a lot of sleepless nights worrying about money, and the crushing burden of developing yearly fund-raising schemes to produce modest sums that are quickly spent. Like many of you I came to realize that we must move from a situation plagued by continuous worry about sources of immediately expendable income, to one in which development of an A.M.U. Endowment Fund will permanently provide us with **interest** funds with which to carry on our malacological commitments. Establishment of the A.M.U. Endowment Fund has been endorsed by the A.M.U. Executive Council, and by the membership of A.M.U. at this meeting. As I see it, is is now up to all those of us who understand the importance of this enterprise to "use our own style" in supporting it.

The eminently worthwhile goals for establishment of the A.M.U. Endowment Fund include: (1) the establishment of a firm, permanent financial base for A.M.U. to enable the organization to meet with confidence immediate and long range exigencies; (2) the development of organizational status that will place us visibly in the mainstream of professional societies in the future; (3) the positioning of A.M.U. so as increasingly to attract, encourage and maintain the burgeoning malacological enterprises of young investigators, **both** professional and amateur; and (4) the continued support by A.M.U. of systematic and conservational concerns, and of good malacological work in land, freshwater, marine and laboratory environments.

The Golden Rule

To return now to the title with which I began these remarks, "Mollusks, the A.M.U., and The Golden Rule"—what connection is there between Mollusks, A.M.U., and certain large concerns of science and society, by way of the Golden Rule? I'm trying to remember when I first learned about the Golden Rule: do unto others as you would have them do unto you. It must have been early in my ontogeny—but it was certainly also during the early grades of Sunday School, when I was growing up in Milwaukee. It was and is to me just about the most exciting ethical, social, and intellectual idea I can think of. In recent years I realize I have not heard of it much. I have wondered, why don't people talk about the Golden Rule? What has happened to the Golden Rule? My Alsatian daughter-in-law, who is a native of Strasbourg, recently commented to me that she had always heard the Golden Rule stated negatively: do **not** do unto others as you would **not** have them do unto you. How did the Golden Rule get so flipped about in coming across the Atlantic Ocean? Be that as it may, to me the positive statement seems more helpful both ethically and intellectually than the negative version. The negative version is proscriptive. The positive version is exhortative: **do** unto others as you would have them **do** unto you.

Thomas Hobbes had his own, Hobbesian—sounding version of the Golden Rule: "Do as you'd be done by." If you look up the term, "golden rule" in the 2nd edition of *Webster's Unabridged Dictionary,* you find it in a religious sense referring to Matthew VII:12:

> "All things therefore whatsoever ye would that men should do unto you, even so do ye also unto them: for this is the law and the prophets."

and to Luke VI:31:

> "And as ye would that men should do unto you, do ye also to them likewise."

"Golden Rule" is also there defined in an arithmetical sense as the rule of proportion or the rule of 3. The latter, as a mathematician colleague has reminded me, is an extrapolation from the Aristotelian concept of the Golden Mean, a concept he pointed out to me is in use today in designing the form of cereal boxes on the grocery shelf so as to make the greatest appeal to us, the buyers, by virtue of their proportion of length to height. It is difficult to ascertain where the Golden Mean came from. Western Civilization has borrowed so much from the early Greeks—could the Golden Rule have been borrowed from Aristotle's notion of temperance?

There seems to be an interesting connection between the Golden Rule and the way in which many of us study animals. Von Uexkull some years ago (von Uexkull, 1909) argued that to know about the world of another organism we must carefully study its inner world (Innenwelt)—its nervous system, its effectors, its sensors—so that we can in our mind's eye insert ourselves into that Innenwelt, look out at the world with **its** sensors, detecting **its** outer world (Umwelt)—the environment relevant to the organism though not necessarily to us. A philosopher colleague to whom I recently described von Uexkull's notion exclaimed that it did indeed sound like application of the Golden Rule to biology. For one can argue that we are counselled by von Uexkull to study other organisms as we, on reflection, would have ourselves be studied.

A few years ago D. R. Griffin, who pioneered work on bat sonar (the means by which bats use echolocation in prey search), wrote an intriguing small book, *The Question of Animal Awareness* (Griffin, 1976). There Griffin inventoried kinds of current research that might point the way to human comprehension of other animals, including J. L. Gould's experimental work with a mechanical bee. The bee Gould made was as carefully constructed an analog as Gould could make of the present human understanding of the nature of a bee, of the Innenwelt and Umwelt of a bee. Gould's hypothesis was that an experimental avenue into the understanding of social behavior in bees was by means of just such a practical, actualized, hypothetical "bee" construct. More recently Griffin has edited a series of papers form the celebrated Dahlem workshop held in Berlin in March, 1981 (Griffin, 1982). His new book, *Animal Mind-Human Mind,* contains varieties of evidence of animal cognition. These include perspectives of neuro-psychological approaches (including analysis of hemispheric specialization); evolutionary ecology of cognition (including risk-benefit assessment by animals); and internal representation, problem solving, and analysis of animal communication.

As a malacologist with huge respect for the beautiful symmetries and plasticities of molluscan nervous systems, as well as much interest in animal behavior, I've been monitoring such developments as the above with an inner sense of *déjà vu.* At such times odds and ends of A.M.U.-meeting conversations recall themselves to me—such as Ginnie Jennewein's account of the summer night she turned on the light, walked into her garage and was startled to discover that a large octopus, which her children had apparently captured earlier in the day, had climbed out of its captive pail of seawater and was walking across the floor of her garage, staring at her balefully with its large, intelligent eyes. (Needless to say, Ginnie's children were bawled out, and the octopus was quickly and respectfully returned to its own habitat.)—Or again, such as the time Clyde Roper fielded the Cephalopod Symposium at the A.M.U.-Louisville meeting in 1980 and I had the chance to learn more about how the winking, blinking, multicolored chromatophores, like an all-over-the-body array of three dimensional tick-tack-toe sets in some cephalopod integuments, effect intraspecific communication by lighting up in directional streaks as one animal raises an arm to another.

Or did I learn this Golden Rule/Innenwelt-Umwelt relation many years ago when I would wake in the middle of the night to hear the front door of our house being quietly opened, then closed. As I heard the soft small footsteps of my then five or six-year-old son, Bob, I would drift back to sleep, calling "Thank you!" to him as I knew he had found a beetle or a spider or a millipede or whatever, and thoughtfully carried it outside where he deemed its habitat to be. I wonder if he knew I was thanking him for teaching me profoundly, what MacIver (1952) has called "the deep beauty of the Golden Rule."

In the study and analysis of reproductive, neurological and behavioral phenomena in the magnificent welter of mollusks, it is easy to integrate experiences such as the foregoing with von Uexkull's admonitions regarding the need for knowledge of the Innenwelt of an animal before we can understand the Umwelt of that animal. And in a different, though I think related sense, I find encounter with a biblical phrase in Exekiel III:15 somehow vindicating:

> ". . . and I sat where they sat and remained there, astounded, among them . . . seven days."

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ABSTRACTS
CONTRIBUTED PAPERS

ANOTHER LOOK AT TORSION. Donald R. Moore, School of Marine Science, University of Miami, Florida.

The Garstang theory that torsion in gastropods is due to a larval mutation has maintained itself against all comers for the last fifty years. This theory, however, ignores the necessary conditions for torsion to take place, and does not allow for time. Instead, torsion must have been a slow gradual process taking a considerable period of time to accomplish.

THE RELATIONSHIP BETWEEN LIVING MOLLUSCAN COMMUNITIES, THEIR DEATH ASSEMBLAGES, AND THE FOSSIL RECORD IN TEXAS BAYS (LAGUNA MADRE AND COPANO BAY). H. Cummins, E. N. Powell, G. Staff and R. J. Stanton, Jr., Texas A&M University, College Station.

Mollusks are important components of the fossil record and serve as the primary data base for many paleocommunity reconstructions. The degree of correspondence between the living molluscan community, the resulting death assemblage generated by the community, and the post-taphonomic assemblage eventually incorporated into the fossil record is poorly understood. We have compared the living community (sampled at six week intervals), the short term death assemblage formed by it, and the shell layer formed by the long term bioturbational condensation of shell material below the bioturbate layer. The living molluscan community is highly variable temporally, whereas the shell layer represents a time averaged accumulation of the molluscan fauna that have lived in the community. Therefore, the molluscan death assemblage is more diverse than the molluscan component of the living community at any given time. All species found living in the community are found in the short term death assemblage. Species found only in the short term assemblage can be divided into two groups: those that are allochthonous inputs into the death assemblage and those previously but not presently members of the community. Differential preservation among the various molluscan species plus time averaging results in a significant change in species composition and abundance in the shell layer relative to either the short term death assemblage or the living community. Some molluscan species present in the living community are absent or poorly represented in the shell layer whereas the importance of others is exaggerated. Therefore, a better understanding of the taphonomic processes affecting molluscan shells is needed before improved accuracy in paleocommunity reconstruction based on them can be achieved.

THE LIFE AND CONTRIBUTIONS OF JAMES GRAHAM COOPER. Eugene Coan, California Academy of Sciences, San Francisco.

James G. Cooper was born in New York in 1830, the son of the early American naturalist William Cooper. After graduating from the College of Physicians & Surgeons in New York City, he became a physician-naturalist for the railroad surveys, exploring the state of Washington in 1852–1854. After additional collecting in Washington, he returned to the east coast in 1856. He participated in a Wagon Road expedition in 1857, hiked through New England's White Mountains in 1858, and explored eastern Florida in 1859. In 1860, he accompanied a detachment of soldiers to the west coast. Once in California, he became associated with the California Geological Survey as its zoologist, and he made extensive collections of plants and animals in the Mojave Desert, coastal southern California, the Channel Islands, the San Francisco area, and the Sierra Nevada. He was also closely associated with the California Academy of Sciences. Living in California until his death in 1902, he chiefly made his living through the practice of medicine, with only his spare time devoted to biology.

Cooper published some 145 books and papers on a variety of subjects. He introduced 138 new zoological taxa, of which 119 are regarded as available, including new species and genera of brachiopods, mollusks, insects, fish, reptiles, birds, and mammals. Some 63% of the names he made available are in current use (with an additional 4% being recognized units under replaced homonyms). A search for the type material of his 114 available species has shown that about half are represented by original material or by neotypes.

Cooper also made significant contributions to biogeography and authored early calls for forest conservation.

BIO-ELECTRONICS: RECAPTURE MADE EASY. Kurt Auffenberg, Florida State Museum, University of Florida, Gainesville.

The use of bio-electronics in the study of animal movement and physiology has increased dramatically in recent years. Although electronic components are now small enough to be used on the larger mollusk species, few references to its use in malacology have been found. A recent study in the Philippine Islands determined some of the limitations and advantages of two bio-electronic techniques (biotelemetric transmitters and light emitting diodes=LED). The continued use and modification of bio-electronic techniques is recommended in the study of molluscan behavior.

STATOCYST STRUCTURE IN PLANKTONIC SQUIDS.

Michael Vecchione, Research and Development, McNeese State University, Lake Charles, Louisiana.

In planktonic *Lolliguncula brevis* which have been stained with alcian blue and cleared with trypsin, the statocysts are simple sacs containing apparently unattached statoliths. Such organs could tell their owners which way is up but would be unsuitable for more sophisticated control of maneuvering. Adult squids sense both linear and angular acceleration with very complex statocysts. I propose that the differences in structure and inferred differences in function of statocysts between adult and planktonic squids can be explained theoretically by ontogenetic changes in their internal and external fluid environments. Cephalopods are among the few taxa that develop pelagically without metamorphosis. Such growth requires that the animals deal ontogenetically with changes in the relative viscosity of their fluid environment; seawater is highly viscous to very small organisms.

Growth rings in the statoliths of cephalopods have shown promise in the difficult task of age determination. The statoliths of very young planktonic squids contain ringlike structures that may be assignable to daily growth.

POSITION OF SQUID *ILLEX ILLECEBROSUS* IN THE ECOSYSTEM.

Tissa Amaratunga, Fisheries Research Branch, Department of Fisheries and Oceans, Halifax.

Among commercially important Cephalopoda, ommastrophid and loliginid squid are the most important. The biology, distribution, and feeding habits of *Illex illecebrosus* are reviewed. Predation is mainly on a few species of crustaceans; predation on fishes and cannibalism are of lesser significance. A predation model is presented that shows an efficient transfer of energy.

HOMOLOGY OF THE FIVE TYPES OF MARGINAL DENTICLES (CHOMATA) OF LIVING OYSTERS (GRYPHAEIDAE AND OSTREIDAE).

Harold W. Harry, Bellaire, Texas.

Internal, submarginal bands, or protochomata, normal to the shell margin, are occasionally seen in *Hyotissa* and some other genera. These seem to be a templet for the five types of marginal denticles present in Gryphaeidae and Ostreidae. Noninterlocking, adjacent, vermiculate ridges, occurring only near the ligament in both valves, are regularly present in *Hyotissa.* Lathe chomata, apparently formed of straight protochomata projecting medially with several fused together, occur in *Hyotissa s.s.* occasionally, below the vermiculate chomata. To varying extent, the vermiculate areas develop a groove parallel to the margin in the left valve, and a corresponding ridge in the right one. Neopycnodontine chomata retain the interlocking ridge and groove, with large, adjacent anachomata (pustules) along the ridge, fitting into catachomata (pits) in the groove. Lophine chomata are minute pustules forming a moderately broad, often interrupted submarginal band completely around both valves, with no pits to receive them in the opposite one. These are aligned on the protochomata, with none, one, two or three on adjacent bands. Ostreine chomata are a single band of anachomata in the right valve with pits to receive them in the left. Chomata are absent in larger specimens of some genera (*Ostrea s.s.*, Striostrea) and entirely absent in post-larval shells of *Crassostrea*.

PHENOTYPIC AND GENOTYPIC VARIATION IN PHYSIOLOGICAL AND GROWTH PARAMETERS OF *MACOMA BALTHICA* (MOLLUSCA, PELECYPODA) FROM AN ARCTIC INTERTIDAL COMMUNITY.

R. H. Green, S. M. Singh, B. Hicks, and **J. McCuaig,** Department of Zoology, University of Western Ontario, London, Ontario, Canada.

The phenotypic and genotypic responses of species and populations to heterogeneous environments provide important information about evolutionary processes. In July 1980 we collected live *Macoma balthica* from populations at two tide levels near Fort Churchill, Manitoba, Canada. Upper lethal temperature tolerances were determined for 209 clams from the mean low water (MLW) population and for 235 clams from the 1.1 m above MLW population, after which all specimens were hard frozen for later electrophoretic analysis. Of 22 loci evaluated, the following were polymorphic: AKP, ACP, EST, LAP, MDH, and ME. Genotypes at these loci were related to tide level, growth rate, tolerance to high temperature, and age. Analysis of shell annual rings was used to verify an earlier report by one of us [RHG] of much faster growth in the higher tide level population.

Growth rate and degree of heterozygosity are both higher at 1.1 m than at MLW. Age structure does not differ between tide levels, but at a given tide level heterozygosity increases with age. Tolerance to high temperature does not differ between tide levels, despite the very different temperature regimes in summer. At a given tide level, individuals with higher growth rates have lower tolerance to high temperatures.

ANOTHER BIVALVE-*APHRODITA* ASSOCIATION WITH COMMENTS ON ADAPTIVE SIGNIFICANCE OF ODDLY SHAPED LEPTONACEA.

Joseph Rosewater, Smithsonian Institution, Washington, D.C.

A third species of Leptonacean bivalve has been found in the respiratory cavity of a polychaete, *Aphrodita,* from off northern Peru in 90-133 m (R/V *Anton Bruun* SEPBOP Cruise 16, sta. 625a; Cruise 18b, sta. 764). Clams are attached by fine byssal threads to elytra of *Aphrodita* similarly to the association described in *Arthritica hulmei* Ponder, 1965. The other *Aphrodita*-clam association was described by Narchi (1969) wherein *Pseudopythina rugifera* (Carpenter, 1864) attaches externally and ventrally. The latter was stated earlier by Pettibone (1953) to occur in the respiratory cavity of the worm and is known also to attach to the crustacean *Upogebia.* This bivalve is reminiscent of species belonging to *Curvemysella* Habe, 1959, i.e., *C. paula* (Adams, 1856), although differing in details of hinge structure and, in mature stages, possesses a strongly crescent-shaped shell which is equivalve, enlarged posteriorly and narrowed anteriorly. Young stages are moderately equilateral, but show progressive changes in shape until the adult inequilateral condition is achieved. Characteristics of shell and soft part morphology indicate placement of this species in the superfamily Leptonacea, family Lasaeidae, following the recent review by Boss (1982): antero-posterior respiratory-feeding current; hinge simple with weakly developed tubercular cardinals; an internal resilium; and inner demibranchs only. Generic and specific affinities are as yet unestablished. The unusual shape may be an adaptation to life in the respiratory cavity of *Aphrodita*. A specimen was observed with the narrow anterior end protruding from between successive parapodia of the worm. Enlargement of the posterior end may provide room for brooding of young, although this is conjecture. Other Leptonacea provide evidence for functional interpretations of their oddly shaped shells. *Curvemysella paula* lives in association with a hermit crab. Similar bivalves with curved ventral margins nestle in apertures and boreholes of gastropod shells where the curvature provides a secure fit; the shell of *Aligena cokeri* Dall, 1909, is grooved from near the umbo to its ventral margin, reflecting a mid-ventral byssal attachment to the tube of the Panamic polychaete *Mesochaetopterus alipes* Monroe, 1933. This somewhat unusual feature was considered an aberration until the clam's life habit was understood.

FLORIDA AND CARIBBEAN *ACANTHOCHITONA* SPECIES DESCRIBED BY REEVE (1847) AND PILSBRY (1893).

William G. Lyons, Florida Department of Natural Resources, St. Petersburg.

Type specimens of *Chiton astriger* and *C. spiculosus,* both Reeve (1847), and *Acanthochites hemphilli, A. rhodeus,* and *A. pygmaeus,* all Pilsbry (1893), were examined. Watters' [1981; Nautilus 95(4):171–177] separation of *Acanthochitona astrigera* (Reeve, 1847) and *A. spiculosa* (Reeve, 1847), previously considered to be synonyms, is confirmed. However, Watters' assignment of *A. pygmaea* (Pilsbry, 1893) to the synonymy of *A. spiculosa* is incorrect; *A. pygmaea* is characterized by incised longitudinal lines on the jugum, whereas such lines are absent on *A. spiculosa,* which also differs from *A. pygmaea* by morphology of spicules of the girdle and sutural tufts and by its larger size (maximum lengths ca. 36 vs. 22 mm). The type-material of *A. spiculosa* does not appear to be assignable to any western Atlantic *Acanthochitona*. Watters' synonymy of *A. rhodea* (Pilsbry, 1893) with *A. hemphilli* (Pilsbry, 1893) is also incorrect. Scanning electron microscope examinations revealed distinct differences in girdle spiculation, valve and tegmental shape, and morphology of tegmental pustules between Florida and northern Caribbean *A. hemphilli* and southern Caribbean *A. rhodea*. Eastern Pacific specimens previously called *A. rhodea* represent an undescribed species. Florida and Caribbean species of *Acanthochitona* presently include *A. astrigera,* a related but smaller undescribed species similar to *A. hirudiniformis* (Sowerby, 1832) of the eastern Pacific, *A. hemphilli, A. rhodea, A. pygmaea, A. andersoni* Watters, 1981, *A. balesae* Abbott, 1954, *A. interfissa* Kaas, 1972 [=*A. balesae fide* Watters], *A. bonairensis* Kaas, 1972 [=*A. communis* Risso (1826) *fide* Watters], and three additional undescribed species from Florida and the Bahamas, for a total of 12 species.

OBSERVATIONS ON THE LIFE HISTORY OF THE WENTLETRAP *EPITONIUM ALBIDUM* IN THE WEST INDIES.

Robert Robertson, Academy of Natural Sciences of Philadelphia, Pennsylvania.

Paper on pages 1–12.

TWO TYPES OF LARVAL DEVELOPMENT IN THE OPISTHOBRANCH *CYLICHNELLA CANALICULATA* (SAY, 1826).

Paula M. Mikkelsen and **Paul S. Mikkelsen,** Harbor Branch Foundation, Inc., Ft. Pierce, Florida.

The cephalaspid *Cylichnella canaliculata,* collected from the Indian River lagoon, eastern Florida, exhibited two types of larval development, often under sympatric field conditions. Field- and laboratory-deposited egg masses contained either small or large eggs. Small (80 μm diameter) eggs, 160–1300 ($\bar{x} = 550$) per mass, hatched in 90 hours as planktotrophic veligers. Metamorphosis was possible 15-20 days after hatching, at 300 μm shell length and 1½ whorls. Large (150 μm diameter) eggs, 20-150 ($\bar{x} = 90$) per mass, were contained in transparent tubes coiled within the mass. These eggs showed capsular metamorphic development, with a veliger possessing reduced velar and median metapodial cilia, and lacking a subvelum. Hatching occurred 200-210 hours after deposition, also at 200 μm shell length, but with only ¾ of a whorl. Larval shell features were clearly distinguishable in the protoconchs of adults. In addition, the adults were separable into two types by shell shape, shell thickness, internal pigmentation, and gizzard plate and radular morphologies. Cross-fertilization attempts in the laboratory were either negative or inconclusive because of a high number of apparently field-fertile adults. However, laboratory-maintained adults never deposited the "wrong" type of egg mass, e.g., adults with planktotrophic type protoconchs produced only planktotrophic developing eggs. The small- and large-egg-producing forms agree with the diagnoses of "*Acteocina*" *candei* and "*Retusa*" *canaliculata,* respectively, as given by Wells and Wells' comparative study (1962, *Nautilus* 75(3):87–93). Because the two species were synonymized by Marcus (1977, *Journal of Molluscan Studies Supplement* 2:1–35) on the basis of identical male reproductive structures, re-examination of reproductive anatomy and compatibility is warranted. Distinct larval and adult morphologies, maintained sympatrically, with no evidence to date of cross-fertilization, suggest the resurrection of *Cylichnella candei* as a valid species.

SPECIALIZED FEEDING IN MITRID GASTROPODS: EVIDENCE FROM A TEMPERATE SPECIES, *MITRA IDAE* MELVILLE.

Alan Fukuyama and **James Nybakken,** Moss Landing Marine Laboratory, Moss Landing, California.

The neogastropod *Mitra idae* is the only member of the family on the California coast. Although suspected of being a specialized carnivore, its food preferences have never been quantified. This study documents the feeding of

Mitra idae on sipunculans. Laboratory experiments and gut analysis of field collected specimens of *Mitra idae* have revealed that it is a specialized predator preferring the sipunculan *Phascolosoma agassizii*.

A PERIWINKLE/SEAWEED ASSOCIATION: EFFECTS OF COMPETITION, FEEDING SPECIALIZATION, AND PREDATION.

Robin Hadlock Seeley, Yale University, New Haven, Connecticut.

Association of *Littorina obtusata* (L.) with brown fucoid seaweeds (*Fucus, Ascophyllum*) has long been observed on Atlantic shores. I have conducted field studies in Maine to answer the following questions: (1) what is the precise pattern of association between *L. obtusata* and fucoid seaweeds? and (2) what selective factors maintain this association? There is striking variation in the degree of association. *Littorina obtusata* is less restricted to fucoids in lower intertidal zones and on wave-exposed shores. Competition: growth and survival of *L. obtusata* in the field were not affected by the presence of *L. littorea* (L.). Feeding specialization: both *L. obtusata* and *L. littorea* grew rapidly in the field on a diet of green algae (*Ulva lactuca*), but their growth on a fucoid algae diet differed. *Littorina obtusata* grew as rapidly on a *Fucus vesiculosus* diet as on an *Ulva* diet, while *L. littorea* grew very little on *Fucus*. Predation: individuals of *L. obtusata* living on fucoid fronds in the field suffered less mortality by *Nucella lapillus* drilling or crab crushing than individuals living on nonfucoid substrata (rock substrata, red algae). In conclusion, variation in the degree of periwinkle/fucoid seaweed association probably reflects spatial and temporal variation in predator activity and the amount of nonfucoid algae available as food. Where *L. obtusata* was found living primarily on fucoids, this association appears to be maintained by high rates of predation on non-fucoid substrata and the unusual ability of *L. obtusata* to feed and grow on fucoid algae.

ECOLOGY OF THE SANDY BEACH GASTROPOD *MAZATLANIA ACICULATA* IN QUIZANDAL, VENEZUELA.

Pablo E. Penchaszadeh, Genoveva C. de Mahieu, Vivianne Farache and Mónica E. Lera, Instituto de Tecnología y Ciencias Marinas, Universidad Simón Bolivar, Venezuela.

Mazatlania aciculata is an important organism in the subtidal sandy beach communities in Venezuela. The population structure is determined by successive recruitment of new generations (four successful recruitments were recorded in one year). The growth, studied by the method of size frequency compositions through time, is rapid, the length of the shell measuring 9 mm (56% of the maximum size in Quizandal) in four months of life. This is the minimal size for sexual maturity. The mean population density varied between 30 to 207 ind./m^2, and the maximum absolute density recorded in Quizandal was 370 ind./m^2. Reproduction starts in November and ends in August. There is a definite correlation of reproduction with water temperature; maximum activity being in March, the coldest month (mean 25.4°C) while minimum activity is in October, the warmest month (mean 28.4°C). The females attach egg-capsules to male shells. In each egg-capsule, 15 to 62 eggs develop (mean number 34). Egg diameter is 210 μm. Eclosion takes place as a free-swimming veliger larva (shell 300 μm in diameter) escapes through an oval aperture. Median lethal temperature ($LT_{50} = 33.5°C$) and median burial temperature ($BT_{50} = 32.5°C$) were determined for periods of exposure up to 96 h, for animals acclimatized at 27°C.

NEW OCCURRENCES OF TURRIDS IN BRASIL WITH DESCRIPTION OF A NEW SPECIES (PROSOBRANCHIA: TURRIDAE).

Eliézer de Carvalho Rios, Museu Oceanográfico da FURG, Rio Grande, RS, Brasil.

In this study, we present a list of 34 new Brasilian coast occurrences of mollusks of the family Turridae collected by the oceanographic vessels *Almirante Saldanha* and *W. Besnard* in depths of 33 to 151 meters.

A new species of *Fusiturricula* was discovered off the Rio de Janeiro coast by fishing boats, at 50 to 55 meters.

THE SEGUENZIACEA: AN UPDATE.

James F. Quinn, Jr., Florida Department of Natural Resources, St. Petersburg.

A summary of the knowledge of the Seguenziacea is presented, compiled from the literature and including unpublished observtions. A synopsis of the taxonomic history of seguenziacean genera is given. A preliminary classification of the superfamily includes 71 nominal species and subspecies in six genera. The known characters of the shells and anatomy are reviewed. The superfamily Segueniacea is shown to be distinct from any other known archaeogastropod or mesogastropod superfamily. This superfamily is characterized by: nacreous shells of archaeogastropod ultrastructure, often complexly sculptured with 0-3 (usually 2 or 3) labral sinuses; modified rhipidoglossate radula (formula 12-4.1.1.1.4-12); paucispiral corneous operculum; epipodial tentacles; monopectinate ctenidium; long intestine with an anterior loop; specialized structures in the reproductive tract (*e.g.*, a well developed penis); and modification of the mantle edge to form distinct incurrent and excurrent siphons. Contents of the intestine indicate that *Seguenzia* is a detritivore.

Ancistrobasis is known from the Eocene, Pliocene, and Recent; *Seguenzia* occurs in the Pliocene and Recent; all other genera are unknown as fossils. Although probably derived from the Trochacea, no direct link with any known fossil or living prosobranch group can yet be established. The superfamily Seguenziacea is here considered to be an isolated offshoot of the Trochacea, independently acquiring advanced anatomical features of a mesogastropod nature as a consequence of extremely small body size and in response to a deep-water habitat.

LITTORINA SAXATILIS (OLIVI) (GASTROPODA: PROSOBRANCHIA: LITTORINIDAE) IN THE VENETIAN LAGOON: ITS VARIATIONS AND LIFE CYCLE, IN RELATION TO ENVIRONMENT.

Alberto R. Torelli, Istituto Ecologia Animale ed Etologia, Università Pavia-Palazzo Botta, PAVIA, Italy.

Available data concerning the horizontal and vertical distribution of *Littorina saxatilis* (Olivi) on the intertidal shores of Venice Lagoon is reviewed. The sex ratio, biotic cycle and female fertility are also studied. A discussion follows about the possible ecological meaning of the polymorphism of *Littorina saxatilis* in Venice lagoon, the typical locality designated in 1792 by Giuseppe Olivi in his description of the species, otherwise so common along the North Atlantic coasts.

The author also points out that the "*tessellata*" morph is far more frequent on the shores exposed to the wave action or to water movements due to motorboats. Unicolored morphs (orange and beige), on the contrary, strongly prevail on less disturbed shores. Ecological variations in size are also taken into account.

EVALUATION OF METHODS FOR SAMPLING FRESHWATER MUSSELS. Sally Dennis, John M. Bates and **Henry van der Schalie,** Ecological Consultants, Inc., Shawsville, Virginia.

Techniques used to sample freshwater mussels include hand-picking, diving, and use of mussel brails. Judicious use of these techniques alone and in combination can provide adequate assessment of mussel populations for most purposes. The brail was used successfully to map mussel beds in the Muskingum River, Ohio, where 176 stations were sampled over 85 river miles. The catch per brail ranged from 0 to 73 (avg. 61). The total catch represented 75% of the species recorded from the river. Quadrat sampling, while useful in the analysis of community structure, is tedious and not suitable for sampling rare species. Twenty square meters sampled in the Clinch River at Kyles Ford yielded 27 (75%) of the 36 species known from this site. Ten additional quadrats produced no new species. Data indicate that brail and quadrat sampling can be used together to establish brailing efficiencies for selected sites, rendering brail catch information more meaningful quantitatively. Such efficiencies established for an area of the Muskingum River compare favorably with the range of 0.2-0.3% reported by Scruggs (1960) for an area of the Tennessee River. The selection of sampling methods should be dictated by the study objectives.

THE DISTRIBUTION AND RELATIVE ABUNDANCE OF *LITHASIA PINGUIS* (LEA), *PLEUROBEMA PLENUM* (LEA), *VILLOSA TRABALIS* (CONRAD), AND *EPIOBLASMA SAMPSONI* (LEA). Arthur H. Clarke, Ecosearch, Inc. Mattapoisett, Massachusetts.

Paper on pages 27–30.

THE DISTRIBUTION OF THE UNIONID MOLLUSKS IN THE STONES RIVER IN CENTRAL TENNESSEE. David H. Stansbery, Ohio State University Museum of Zoology, Columbus, **Ralph M. Sinclair,** Environmental Protection Agency, Cincinnati and **Billy G. Isom,** Tennessee Valley Authority, Muscle Shoals.

The Stones River of the Nashville Basin in central Tennessee is favored by a number of factors conducive to the presence of freshwater mollusks both in diversity of species and numbers of individuals. The river, amply shaded in its central and upper reaches, flows over limestone bedrock for nearly its entire length and receives significant amounts of cool, mineral-rich water from subterranean aquifers in the central part of its basin. Its overall gradient provides a good balance of riffles, runs and pools and an abundance of rooted aquatic plants assure large areas of stable yet penetrable substratum.

The impending threat of the Percy Priest Dam impounding nearly all of the Stones River main stem inspired our first concerted efforts to determine its unionid fauna. A total of 33 sites were collected in the years 1964 to 1966 and an additional 24 sites have been studied in the intervening years.

The Percy Priest Dam and impoundment have become realities. The effect of this impact upon the riverine mollusks is presently under study. The objective of this study, however, has been to determine the pre-impoundment composition of the river's unionid fauna. Our collections, in addition to a careful examination of the literature reveal evidence indicating that at least 45 species of unionids lived within the Stones River in recent times.

WINNING WITH MUSSELS: A CASE HISTORY. John M. Bates, Sally D. Dennis, and **Henry van der Schalie,** Ecological Consultants, Inc., Shawsville, Virginia.

Fresh water mussels were used successfully to monitor effects of an industrial discharge in the Muskingum River, Ohio, and to establish environmental damages resulting from discharge of copper into the river. Three years of study of the commercial resources of the Muskingum River (1967–70) provided baseline data on mussel distribution and population densities throughout the river and allowed for an accurate determination of the value of the resource. Following a reported mussel kill in 1972, the fauna was re-evaluated and damage to the resource assessed. Laboratory and field studies were designed specifically to determine effects of copper on fresh water mussels and to establish a cause and effect relationship between the industrial discharge and the mussel kill. Interdisciplinary studies included water and sediment analysis and periphyton sampling and analysis in addition to the mussel studies. The combination of background data with laboratory and field monitoring allowed for successful litigation of an environmental damage suit against the polluting industry.

THE MOLLUSCAN FAUNA OF THE ELK RIVER IN TENNESSEE AND ALABAMA. Steven A. Ahlstedt, Tennessee Valley Authority, Division of Air and Water Resources, Norris.

Paper on pages 43–50.

THE LITTLE RIVER UNIONID FAUNA AND ITS IMPLICATIONS FOR UNIONID BIOGEOGRAPHY. Arthur E. Bogan, Department of Malacology, Academy of Natural Sciences, Philadelphia, Pennsylvania and **Lynn B. Starnes,** Tennessee Valley Authority, Knoxville.

The unionid fauna of the Little River, Blount County, Tennessee was surveyed to test the hypothesis that the headwater limit of unionid distribution may be predicted by an examination of a physiographic gradient of the stream. Bivalves should not be found above the upstream section of the river where there is a sharp increase in the stream gradient. Our survey documented 11 species of unionids and the literature records the former occurrence of eight additional species not encountered in the survey. Our data for the Little River are consistent with those published for the Powell, Clinch, and Holston Rivers and the Little South Fork of the Cumberland River; the last bivalve species was collected downstream of the sharp continuous increase in gradient. Numerous studies of the fish fauna in the eastern United States have shown that longitudinal diversity in fish species is correlated with stream order, gradient, and drainage area. Fish species diversity increases with increasing stream order. This is important since the unionid glochidia are parasitic on fish gills and dependent on the fish for distribution. Factors limiting fish would directly limit the unionid distribution. From the data on the longitudinal diversity in fish species, the unionids should exhibit a regular pattern of longitudinal diversity similar to the fish. This pattern should be additive from the headwaters downwards and correlated with increasing stream order. Longitudinal diversity of aquatic macroinvertebrates also has been shown to be positively correlated with stream order. This pattern of longitudinal diversity might be explained by changes in several factors: 1. gradient, 2. water temperature, 3. substratum particle size, 4. size of organic particles, 5. water flow fluctuations, 6. water hardness. Stream gradient decreases with increasing stream order as does overall substratum particle size and size of suspended organic particle. As the stream increases order the fluctuation of the stream flow decreases and the number of niches increases. It is suggested that no single limiting factor determines the headwater limit of unionids, but an interaction of the above factors coupled with fish distribution.

OBSERVATIONS ON *LAMPSILIS ALTILIS* (CONRAD) AND *L. PEROVALIS* (CONRAD) FROM THE MOBILE RIVER SYSTEM. Robert W. Hanley, The University of Alabama, Tuscaloosa.

Conrad and Lea described six species of rayed unionid clams from the Mobile River system between 1834 and 1865. Simpson placed these taxa in the genus *Lampsilis.* Most recently only one of these species, Conrad's *altilis,* has been considered valid. After examining over two hundred specimens, I feel that both *altilis* and *perovalis* deserve recognition; while Lea's names represent ecophenotypes of Conrad's species, and hence should be placed in synonomy. The shell of *altilis* tends to be more elongate than that of *perovalis,* and the lateral teeth of the former are straight whereas the lateral teeth of *perovalis* tend to be curved. Whether *altilis* and *perovalis* belong in the genus *Lampsilis* is questionable. The marsupium of *altilis* occupies the entire outer demibranch, a characteristic of the Anodontinae. However, *altilis* also has traits of the Lampsilinae: sexual dimorphism of the shell, and demarcation of the marsupial ovisacs by sulci. Until more thorough studies of the anatomy and glochidia of these species are completed, it is best to retain them in *Lampsilis* s.l.

MOLLUSKS FROM AN ARCHAEOLOGICAL SITE IN WOODFORD COUNTY, KENTUCKY. Samuel M. Call, Kentucky Natural Resources and Environmental Protection Cabinet, Division of Environment Services, Frankfort and **Kenneth Robinson,** University of Kentucky, Lexington.

Paper on pages 31–33.

UNIONID MOLLUSKS OF THE MISSOURI RIVER ON THE NEBRASKA BORDER. Ellet Hoke, West Des Moines, Iowa.

Paper on pages 71–74.

NAIAD MOLLUSK POPULATIONS (BIVALVIA: UNIONIDAE) IN POOLS 7 AND 8 OF THE MISSISSIPPI RIVER NEAR LA CROSSE, WISCONSIN. Marian Havlik, Malacological Consultants, La Crosse, Wisconsin.

Paper on pages 51–59.

ORGAN GROWTH IN BIVALVES: AN ANALYSIS OF GROWTH PATTERNS IN A TOPOTYPIC POPULATION OF *ELLIPTIO LANCEOLATA* (LEA, 1828). C. Clifton Coney, Richard H. Moore, and **Silvard P. Kool,** University of South Carolina, Coastal Carolina College, Conway.

Forty females and forty-two males of topotypic *Elliptio lanceolata* collected from the Tar River, North Carolina, ranging from one to five years of age, were selected for growth analysis. Specimens were prepared utilizing methodology described by Coney, Moore, and Kool (1981).

Previously undescribed structures found within stained inner demibranchs are reported. Mature septa arise from immature septa (quasisepta) located within the anteriormost inner demibranch. As determined by maturity and frequency of septa, the anteriormost inner demibranch is younger, while the posteriormost portion is older. As growth stress builds within the demibranch, structurally supportive vertical thickenings of tissue (columna) appear. There are three growth stages of columna: (1) distal columna primordia, which develop from the distal demibranch margin, (2) proximal columna primordia, which develop from the proximal demibranch margin; these two structures eventually joining together as (3) mature columna. While mature septa arise from the anterior quasisepta, septa may also develop from mature columna as a result of growth stress.

The greatest change in growth rate occurred in individuals between two and three years of age. Demibranch length and height were correlated ($P < 0.001$) with age. Asymmetric growth of the inner demibranch is probable, as demibranch length increased at a faster rate than demibranch height. The number of septa, filaments, distal and proximal columna primordia were correlated ($P < 0.001$) with age, however the number of quasisepta were inversely correlated ($P < 0.001$) with this factor. Females had longer gills than males ($P < 0.05$), with more distal columna primordia ($P < 0.05$), and more septa and filaments ($P < 0.01$) than males. Sexual dimorphism was fully developed by the third year of growth. Both anal and branchial papillae increased in numbers with age ($P < 0.001$) but were not significantly correlated with sex.

This research was supported in part by a grant from the U.S.C. Coastal Carolina College Faculty Development Fund funded by the Horry County Higher Education Commission.

COMPARISONS OF MORPHOMETRIC AND SOFT ANATOMY CHARACTERS BETWEEN TOPOTYPIC POPULATIONS OF *ELLIPTIO LANCEOLATA* (LEA, 1828) AND *E. ANGUSTATA* (LEA, 1831).

Richard H. Moore, C. Cliff Coney, and **Michael R. Creitz**, University of South Carolina, Coastal Carolina College, Conway.

Collections of 209 topotypic *Elliptio lanceolata* (Lea, 1828) from the Tar River, North Carolina, and 80 topotypic *E. angustata* (Lea, 1831) from the Congaree River drainage, South Carolina, were subjected to a multivariate analysis of shell morphometrics. Nine three-year-old females of each species, all eight three-year-old male *E. lanceolata,* and all seven three-year-old male *E. angustata* were used in an analysis of soft anatomical characters.

Fourteen measurements were made on each pair of valves. Linear measurements were logarithmically transformed and principal components extracted from the correlation matrix. The two species separated almost completely in multivariate space defined by the first two principal components. Examination of loading coefficients showed the two species differed in the angle between the left pseudocardinal teeth, the angle between the right pseudocardinal teeth, the right interdentum angle, and the anterior development parallel to the hinge line. A multiple discriminant analysis of these data assigned all but one *E. lanceolata* and all *E. angustata* to their correct taxon.

A number of obvious distinctions were noted in the soft anatomy. The mantle of *E. lanceolata* was plain and almost transparent, while that of *E. angustata* was orange and darkly mottled. The posterior gill ligament was short, thick, and sinuous in *E. lanceolata,* but long, thin, and straight in *E. angustata.* Anal papillae were longer and spaced further apart in *E. angustata.* Branchial papillae in *E. lanceolata* were stout and almost pyramidal in shape, while in *E. angustata* they were thin, and finger-like. *E. angustata* males typically possessed dark pigmented areas at the bases and between their branchial papillae. *E. lanceolata* possessed broad demibranchs, while *E. angustata* had narrower, elongated, tapering demibranchs.

The species differed significantly in the number of branchial papillae, total gill filaments, and in the numbers of supportive tissues in the gill. Total anal papillae and numbers of septa did not differ.

In conclusion, *E. angustata* (Lea, 1831) should be resurrected as distinct from *E. lanceolata.* Their forms are separable in their shell morphometrics; however, soft anatomy characters are more easily observed and quantified.

ECOLOGICAL RELATIONSHIPS OF SYMPATRIC SPECIES OF LAMPSILINAE (BIVALVIA: UNIONIDAE) IN THE WACCAMAW DRAINAGE OF EASTERN NORTH AND SOUTH CAROLINA.

Hugh J. Porter University of North Carolina, Morehead City and **Karen J. Horn,** Marshall University, Huntington, West Virginia.

Paper on pages 61–66.

ALLOMETRIC GROWTH AND SEXUAL DIMORPHISM OF *VILLOSA VILLOSA* AND *ELLIPTIO ICTERINA* (PELECYPODA: UNIONIDAE) FROM LAKE TALQUIN, LEON CO., FLORIDA.

M. Bowie Kotrla and **Frances C. James,** Department of Biological Science, Florida State University, Tallahassee.

The objectives of the study were 1) to find shape variables by which functional sex may be deduced from shell characters, and 2) to describe allometric growth. *Villosa villosa* (Wright, 1898) and *Elliptio icterina* (Conrad, 1834) were selected as examples of species having shells with obvious and cryptic sexual dimorphism, respectively. Measurements of the length, width, and distance from umbo to perimeter at various angles from the hinge line were taken. Maximum distance from umbo to perimeter, and angle at which it occurs were also measured.

Under the lognormal assumption, differences among shape variables, such as log x–log y, can be tested with parametric statistical tests. Of 13 shape variables, seven were found to be significantly different between males and females of *V. villosa* by T-tests, and 100% of these individuals were correctly classed as to sex by discriminant analysis. Linear regressions of shape on size reveal a trend from an ovate to an elliptical shape as size increases in *V. villosa.* The rate at which this occurs in the posterior region of the shell is greater in females than in males. The shape change in *E. icterina* during growth is more complex than that of *V. villosa.* Rate of change is greater in males than in females as measured by eight of 13 variables.

HISTOLOGY OF THE TESTIS OF *TAREBIA GRANIFERA* (LAMARCK).

Harold D. Murray, Trinity University, San Antonio, Texas.

Males were unknown in North American *Tarebia granifera* until 1977 when spermatogenesis was observed in electron micrographs in association with the digestive gland. Later studies revealed motile eupyrene and oligopyrene sperm in 4.7% of the population. The histology of *T. granifera* testis is unreported.

Testis and associated digestive gland were fixed in Bouin's solution, dehydrated in a graded alcohol series, and paraffin embedded. Sections were cut at 7 μm and stained with Delafield's hematoxylin and eosin.

The testis lies on top of the digestive gland from which it is separated and is composed of numerous V-shaped folds with their apices facing the digestive gland. In females, the tubular, branched ovary is embedded in the digestive gland and typically follows the columellar aspect of the animal.

The testis grows from the first whorl of the animal displacing up to ⅔ of the digestive gland. Small vasa efferentia leave the apex of each V in the first whorl and are absent in other areas. These vasa unite to form a nonmuscular sperm duct. Each V-shaped area of the testis shows sequential stages of spermatogenesis with mature sperm at the apex. Primordial cells are at the cap of the V next to the mantle.

The testis of *T. granifera* enlarges from the first whorl of the animal, occupies up to ⅔ of the digestive gland, has no intimate contact with the digestive gland, and appears to have an embryological origin unrelated to the ovary.

THE LIFE HISTORY AND PRODUCTION OF IMMATURE *CORBICULA FLUMINEA* (MOLLUSCA: BIVALVIA), IN LAKE NORMAN, NORTH CAROLINA. James J. Hall, Duke Power Company, Charlotte, North Carolina.

The life history and annual production of the Asiatic clam *Corbicula fluminea,* were determined in the littoral (~4 m) and sublittoral (~8 m) zones of Lake Norman, North Carolina, from February 1978 through January 1979. *C. fluminea* were collected from four locations in each zone using a modified Petersen grab (258 cm^2). In Lake Norman, *C. fluminea* had a growing season greater than nine months, from 22 March 1978 to 8 January 1979. Due to insignificant numbers of large clams ($\geq$ 6.5 mm) collected, production estimates and mean densities were estimated only for *Corbicula* $\leq$ 6.0 mm; estimates were therefore probably conservative. Production estimates were multiplied by two to account for two generations produced each year (based on one year growth study). Higher annual production (516 mg/m^2/yr) and P/B ratio (26.4) of *Corbicula* occurred in the littoral zone, compared to the annual production and P/B ratios in the sublittoral zone, which were 182 mg/m^2/yr and 16.4, respectively. *C. fluminea* in the littoral zone had the higher mean annual density (2040/m^2) and mean annual biomass (20 mg/m^2) compared to the mean annual density (891/m^2) and mean annual biomass (11 mg/m^2) of *C. fluminea* in the sublittoral zone.

ELECTROPHORETIC VARIATION IN *CORBICULA*. M. J. McLeod, Belmont Abbey College, Belmont, North Carolina.

The Asian clam *Corbicula* was introduced into this country around 1930 in Washington state. Since that time it has spread south and east across the country. There is only one published multipopulation electrophoretic survey of *Corbicula* in this country. In that, Smith et al. (1977) found no genetic variation in or between any populations and attributed this to the introduction being a founder event. Even if it is a founder event, however, 40 years should be enough time for some mutations to accumulate and to be magnified by drift and/or subsequent founder events. In a previous study of a single population at seven loci, I found a small amount of electrophoretic variation. Here I report on a larger study involving several populations that are geographically widely distributed. Populations were analyzed by horizontal starch gel electrophoresis. The results of this work indicate the following: 1) There is electrophoretic variation in most, if not all, U.S. populations of *Corbicula*; 2) Variation between populations exists but at different enzymes between different populations. While polymorphism is present, heterozygosity is rare, at least at those loci coding for soluble enzymes. These data suggest that *Corbicula* may be an excellent species to use to follow the accumulation of genetic variation both within and between populations over time. This project was supported by a grant from Research Corporation.

COMPARATIVE FUNCTIONAL MORPHOLOGY OF CILIA OF *CORBICULA* (BIVALVIA: CORBICULIDAE): POSSIBLE CRITERIA FOR EFFECTOR AND PUTATIVE SENSORY TYPES. Louise Russert Kraemer, University of Arkansas, Fayetteville.

Paper on pages 13–20.

ARE THE *BULINUS* SNAILS PROTANDRIC HERMAPHRODITES? Shi-Kuei Wu, University of Michigan, Ann Arbor and University of Colorado, Boulder.

African freshwater *Bulinus tropicus* snails have been demonstrated morphologically to be protandric hermaphrodites (Wu, 1972). This study was intended to demonstrate it in their behavior. Mating behavior of two, three and four snails of different sizes were observed for normal mating sequences and preferences. In two-snail experiments over a six-week period: in 60% of the experiments the *B. tropicus* found its mate and copulated within 30 minutes after being released into petri dishes. A "male" may mount on its partner from any direction. In all cases, it must move posteriorly to the apex of the partner, then turn around and move anteriorly toward the left side of the partner to assume the copulatory position, often everting its penis at this time. The copulation time lasted variably one to 12 hrs; matings lasting six hours were fairly common.

In two-snail experiments between a small albino and a large pigmented snail, 59 out of 75 matings observed were small snail on large snail (mean size difference at the beginning and the end of the six week period was 1.1 mm). In two-snail experiments between a small pigmented and a large albino snail, 45 out of 101 matings observed were small snail on large snail (mean size difference at the beginning and the end of the six week period was 0.1 mm). Direct measurement of 74 pairing snails in the aquaria indicated 68 pairs with the small snail acting as "male", two pairs of the same size and four pairs with the large snail acting as "male".

Twenty experiments using three snails (one small and two large) and 10 experiments using four snails (two small and two large) showed that *B. tropicus* mated preferentially and mutually on the same size snails, or the smaller one acted as "male".

Overall, the smaller snails tend to mate on larger snails behaviorally, and the male organs are more developed than the female organs for younger snails morphologically. It is concluded the African *Bulinus tropicus* snails are protandric hermaphrodites.

HISTOCHEMICAL AND ULTRASTRUCTURAL ANALYSIS

OF THE MORPHOLOGY AND FUNCTION OF THE SPERMATHECA OF *BIOMPHALARIA GLABRATA*. Steffen H. Rogers and **Richard L. Reeder,** University of Tulsa, Tulsa, Oklahoma.

The function of the spermatheca has been a long standing question. These authors have reported previously that the spermatheca is a digestive organ in several species of terrestrial snails. The same appears to be true in *Biomphalaria* even though the morphology of this organ in the aquatic species is somewhat different from the terrestrial. Histological and ultrastructural analysis demonstrated that the spermatheca is a thin-walled luminal organ. From the lumen outward there exists a four-layered wall: one layer of columnar epithelial cells with an absorptive surface, basal lamina, a thin layer of muscle cells, and an intermittent covering of cells with unusual morphology. The lumen is filled with debris. In *Biomphalaria,* each epithelial cell has the same morphology as opposed to terrestrial species where both absorptive and goblet cells can be demonstrated. The columnar cells have a thick zone of mitrochondria just below the microvilli, a zone of massive vesicles, a nuclear zone, and a zone of rough endoplasmic reticulum (ER) and Golgi. Enzyme activity exists within the lumen and the organ wall. Gel digestion techniques were used to demonstrate the presence of DNAase, RNAase, and protease activity in the lumen of the spermatheca. Acid phosphatase activity is localized in the rough ER area of the columnar cells. Alkaline phosphatase activity can be demonstrated in the microvilli zone and in the cells of the outer casing. ATP-ase is localized in the muscle and mitochondrial zone of the epithelial cells. Histochemical techniques were used to demonstrate positive reactions to periodic acid Schiff, Feulgen, and Sudan black in both the lumen and the organ wall.

A PRELIMINARY REPORT ON THE MOLLUSCA OF THE BUFFALO NATIONAL RIVER. **Mark E. Gordon,** University of Arkansas, Fayetteville.

The Buffalo River is one of the few rivers in Arkansas for which any previous published survey of the molluscan fauna exists. Meek and Clark (1912) reported 22 species of mussels from a survey of about two-thirds of the rivers's length. When the river was incorporated into the National Park Service in 1972, a series of studies were initiated to assess the flora, fauna, and general ecology of the Buffalo River valley. The Mollusca were noted only as an occasional component of the benthos; when, in fact, they are often the dominant organisms in both terms of numbers and weight. This study was intended to correct this oversight and examine any changes that may have occurred in faunal composition over the last 60 years. Thirty-five molluscan species have been identified from recent intensive sampling. This represents seven gastropods and 28 bivalves. With the exception of *Corbicula fluminea,* this probably does not represent an actual increase in the faunal diversity since 1910.

RELATION OF *GIZZARD STONES* TO TOXICITY OF COPPER. **Marc J. Imlay,** Columbia National Fisheries Research Lab., US Fish and Wildlife Service, Columbia, Missouri.

An interaction with food, sediment, copper, and snails was discovered with *Pomacea paludosa* and *Stagnicola sp.*

Sediment took copper out of the water thereby allowing it less time to kill the snails.

Feeding the snails lettuce doubled the toxicity of copper in the presence of sediment and only in the presence of sediment.

One possible biological explanation for the effect of lettuce in the presence and only in the presence of sediment on the toxicity of copper is that *Pomacea* and *Stagnicola* search the sediment for sand or grit with which to triturate the food in the gizzard.

Copper associated with ingested sediment when the snails fed could easily enter the tissues of the snails and thereby become toxic.

REGIONAL SPECIES RICHNESS IN LAND SNAILS: IS BAJA CALIFORNIA A PENINSULA? **Carl C. Christensen,** Bernice P. Bishop Museum, Honolulu, Hawaii.

It has been demonstrated that in birds and mammals of Baja California species richness is greatest at the base of the peninsula, decreasing southward to its tip. This decrease has been termed the "Peninsular Effect" and has been attributed by some to the presence of an equilibrium between extinction and recolonization. Patterns of species richness in lizards and snakes have been shown not to be consistent with this equilibrium model: here a transition is seen between distinct northern and southern faunas of approximately equal diversity, the southern elements owing their presence to the tectonic history of the region rather than to an extinction/recolonization process. Among larger land mollusks (Haplotrematidae, Spiraxidae, Bulimulidae, Ammonitellidae, Oreohelicidae, and Helminthoglyptidae) a similar pattern is seen in which northern and southern portions of the peninsula support dissimilar mollusk faunas, the central peninsula being a zone of transition. Regional species richness is highest in areas of greatest precipitation, particularly in the southern peninsula where autochthonous speciation has resulted in a significant increase in species richness over evolutionary time. No Peninsular Effect is evident, and the high level of endemism characteristic of these snails indicates that the peninsula, particularly its southern portion, supports a fauna strongly isolated from those of surrounding regions. In comparison with the vertebrates of the region, the larger terrestrial mollusks appear to be less vagile and exhibit a much stronger propensity for autochthonous speciation, factors that probably account for much of the observed differences between the diversity patterns of these groups.

LAND SNAILS (POLYGYRIDAE) AS A SOURCE OF ANTI-A AGGLUTININ FOR TYPING HUMAN BLOOD. **Charles D. Miles,** University of Missouri-Kansas City and **Malcolm L. Beck,** Community Blood Bank of Greater Kansas City, Missouri.

Snails belonging to a number of European aquatic and terrestrial species have been shown to possess anti-A agglutinin, which appears to be restricted to the albumen gland and eggs. *Helix aspersa, Cepaea nemoralis* and *C. hortensis* possess especially strong agglutinin activity. We investigated nine species of land snails from northern Missouri and northeastern Kansas to determine if any possess anti-A agglutinin. *Succinea ovalis* (Succineidae), *Anguispira alternata* and *A. kochi* (Endodontidae) were negative. All six species of Polygyridae tested did possess the anti-A agglutinin, including *Triodopsis albolabris alleni, T. multilineata, Mesodon elevatus, M. thyroidus, M. clausus* and *Allogona profunda.*

That certain species of U.S. land snails possess highly potent anti-A agglutinin is of more than theoretical interest. Snail anti-A agglutinin has replaced human material in many European blood transfusion centers. Perhaps as much as half the blood transfused in England is done so with snail anti-A agglutinin. The fact that all species of Polygyridae tested possess anti-A agglutinin may be of phylogenetic significance. Perhaps it is a family characteristic. Preliminary data suggest that *M. elevatus* is similar to *H. aspersa* and *H. pomatia* in that its anti-A reacts with both T and T_n red cells. The other polygyrids tested react with only T_n cells but not T cells. (This work was supported in part by a UMKC Faculty Research Grant.)

SEASONAL CHANGES IN THE REPRODUCTIVE ANATOMY OF *TRIODOPSIS TRIDENTATA TRIDENTATA* (PULMONATA: POLYGYRIDAE). Kenneth C. Emberton, University of Chicago, Chicago, Illinois.

A series of collections was made March-July, 1979 at Strouds Run State Park, Athens, Ohio. The reproductive systems of 57 specimens (1-6 per collection) having reflected peristomes were dissected free, and each reproductive organ was ranked according to relative volume. The hermaphroditic duct, prostate, albumen gland, uterus, and spermatheca showed significant seasonal variation. Three principal components, labeled *mating readiness, egg production,* and *allosperm absence,* explained 84% of this variation. Results support the following conclusions (1) A protandric reproductive cycle, with overwintering of both adults and juveniles (2) Decoupling of the organ suites used for a) sperm exchange, b) egg production, and c) allosperm storage (3) Strong contributions to the seasonal pattern of variation by late-maturing, unmated, and sexually dormant individuals.

HISTOLOGY OF THE SEMINAL RECEPTACLE COMPLEX IN *MESODON ZALETUS.* Richard L. Reeder and **Steffen H. Rogers,** University of Tulsa, Tulsa, Oklahoma.

The microanatomy of the seminal receptacle complex has not been investigated in detail in any polygyrid land snail. In general, members of the Polygyridae conform to the pattern described by various workers for members of the Helicidae. In *Mesodon zaletus* there is an enlarged chamber (ciliated hood) and a series of separate diverticula enclosed within a common connective tissue-muscle layer. These empty into a common chamber that is joined by the hermaphroditic duct. This common chamber is an apparent fertilization chamber and leads into the sperm-oviduct. The epithelium of the ciliated hood is scalloped with alternating areas of tall columnar cells having long cilia or stereocilia and cuboidal cells devoid of cilia. The diverticula are embedded in the adjacent connective tissue-muscle mass along with the terminal portion of the hermaphroditic duct. These diverticula expand into dilated sacs at their terminus and are lined with a cuboidal epithelium throughout. Once the lower hermaphroditic duct departs from the connective tissue mass it is expanded as a seminal vesicle. It is also lined with an epithelium having alternating areas of tall and low cells, the taller cells with apparent cilia. We have investigated this complex in other polygyrid snails (*Ashmunella chiricahuana, Triodopsis albolabris, Stenotrema fraternum*) and the above described pattern appears consistent except that there is a variable number of small diverticula.

PROPOSED ANALYSIS OF SHELL COLOR AND PATTERN CHARACTERS IN *LIGUUS.* Barry Roth, California Academy of Sciences, San Francisco, and **Arthur E. Bogan,** Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.

The existing taxonomy of the Florida land snail *Liguus fasciatus* (Mueller, 1774), based on total phenotypes considered typologically, has hampered understanding of the species' variability. Elements of shell color and pattern inherit separately and can be expressed by an alphanumeric code.

A model of *Liguus* biogeography based on the fragmentation of an originally widespread, homogeneous, and phenotypically diverse population is proposed, in contrast to the traditional model of random dispersal *via* hurricane.

SIMULTANEOUS CHARACTER CONVERGENCE AND DIVERGENCE IN WESTERN AUSTRALIAN LAND SNAILS. Alan Solem, Field Museum of Natural History, Chicago, Illinois.

The Napier Range, east of Derby, Western Australia, is a narrow ridge of exposed Devonian limestone reefs with many camaenid land snails. Two genera, *Amplirhagada* Iredale, 1933, and *Westraltrachia* Iredale, 1933, have four and seven species. There rarely is sympatry within a genus, but essentially species of both genera were found at every station.

Amplirhagada, ranging through much of the north Kimberley, is at its southern limit. Its shell is larger in size and whorl count, proportionately higher, and has continuous red spiral color bands. Species of *Amplirhagada* aestivate either sealed to something or free-sealed on the soil surface. *Westraltrachia,* confined to the Napier Range and the chains of limestone hills extending south-east, typically is smaller in size and whorl count, more depressed in shape, and has a patterned color or irregular brown markings. It feeds on both plant debris and rock face seepage zone blooms of algae. *Westraltrachia* always aestivates as a free sealer.

In the Napier Range, *Westraltrachia* has specialized in scraping from the algal films and undergone dramatic changes in jaw and radular structures. The change is partial in the south-east Napier Range, complete in the taxa living west of Windjana Gorge. *Westraltrachia* shows partial preadaptation for this shift. In sympatry with *Amplirhagada* under conditions of increased abundance of algal-films, it has diverged in feeding structure and resource use.

Conchological convergences involve first reduction, then loss of color pattern in the south-east, size change in the central area, then evolution of chalk-white shells that are almost identical in size and shape in the north-west Napiers. The new convergent morphotype is different from both ancestral models. There is no evidence of unusual predation pressure to explain why this massive shell convergence occurred.

SHELL MORPHOLOGICAL VARIATION IN *PUPILLA* (PULMONATA: PUPILLIDAE). **Peter B. LaRochelle,** University of Colorado Museum, Boulder.

The taxonomy of the genus *Pupilla* is based entirely on shell characters: compliment of teeth (lamellae, folds, plicae, etc.), shell dimensions, number of whorls, and other calcifications within and behind the peristome. Pilsbry (1948) recognized six North American species, namely *P. sonorana, P. blandi, P. muscorum, P. hebes, P. syngenes,* and *P. sterkiana* of which the first five are closely allied. *P. blandi, P. muscorum,* and *P. hebes* have been reported from Colorado.

More than 100 lots of Colorado *Pupilla* were examined comprising over 600 specimens. Adult tooth number is highly variable between and within lots and can range from zero to three within a single lot. Similarly, the crest behind the peristome may be absent to well formed. There appears to be no strong relationship between tooth number and either shell height, shell diameter, number of whorls, or crest formation.

The distribution of the various dental forms of *Pupilla* in Colorado was determined. The three toothed form (*P. blandi*) is found both east and west of the continental divide and is the predominant form on the western slope. Poorly dentate forms (*P. muscorum* and *P. hebes*) are found primarily east of the continental divide along the front range of the Rocky Mountains with only occasional specimens being found on the western slope.

In light of the wide variability in certain shell characteristics of *Pupilla* in Colorado and the poor relationship between tooth number and other shell features, I hypothesize that *P. blandi, P. muscorum,* and *P. hebes* are variations of a single species, *Pupilla muscorum.* Variables such as climate, soil mineral content, predation, and the nature of dispersal events may influence the frequency of the various shell forms exhibited by this species.

DISCOVERY OF RECENT *HENDERSONIA OCCULTA* (SAY) IN MISSOURI. **William Hay,** Jefferson City, Missouri.

Hendersonia occulta (Say) was abundantly and widely distributed during the Pleistocene and is commonly found in loess deposits in Missouri. Its present distribution is rather disjunct and widely separated localities have been reported from Pennsylvania, North Carolina, Virginia, Tennessee, Illinois, Wisconsin, Minnesota, and Iowa. This report represents the first recent specimen of *H. occulta* recorded from Missouri.

ENVIRONMENTAL RECONSTRUCTION OF THE HOLOCENE OF THE TEXAS PANHANDLE: 10,000 YEARS OF TERRESTRIAL AND FRESHWATER GASTROPODS. **Raymond W. Neck,** Texas Parks and Wildlife Department, Austin.

The Eastern Caprock Escarpment presently contains a gastropod fauna characterized by low species diversity communities that are restricted to isolated patches of favorable microhabitats. Sequential sediments from 10,000 B.P. to the present from the Lake Theo Site have allowed an analysis of a gastropod fauna that has been reduced substantially by local extinction. The extirpation process appears to have been a three stage process. Snails suffering extinction at approximately the same time are generally from the same general geographical area. Extirpated species include those now occurring in more eastern areas and those now restricted to areas to the north. Snails present in the oldest levels could exist at the Lake Theo Site with a more equable regime of precipitation and an amelioration of summer temperature extremes. Denser deciduous woodlands probably occurred over larger areas than occur today. Older sediments indicate presence of mesic to saturated soils in these woodlands. An intensive survey of the area surrounding the Lake Theo Site has revealed a depauperate modern snail fauna of low diversity.

LATE QUATERNARY LAND SNAILS FROM THE NORTH COAST OF JAMAICA. **Glenn A. Goodfriend,** Department of Zoology, University of Florida, Gainesville.

The historical biogeography of Jamaican land snails is examined, based on four late Quaternary deposits from small solution holes at the Green Grotto Caves on the central north coast of the island. Amino acid racemization/epimerization dating (based on alloisoleucine/isoleucine ratios) indicates that the oldest deposit probably dates from the glacial period before last. Two deposits are of Wisconsinan age and the fourth is of late Holocene age (< 3000 yr). Evidence is presented that Pleistocene conditions at the site were cooler and drier than at present.

A number of species (including north coast endemics as well as currently widespread species) occur in all four deposits and are still living at the site. These species appear to have persisted at this locality through the late Pleistocene and Holocene. Other species in the deposits no longer live at the site or surrounding areas. For example, five species that occur only in the Pleistocene deposits are currently limited to the cooler and moister interior plateau. The extension of the ranges of these species down to the coast during the Pleistocene is probably associated with the cooler temperatures of that time. *Urocoptis brevis,* now limited to the dry south coast and the driest part of the north coast (some 25 km west of the site), occurs in one Pleistocene deposit. The eastward extension of its range at that time may be associated with the drier climatic conditions. *Sagda montegoensis,* abundant in the Pleistocene deposits, is now endemic to a small area at the western end of the island. This change in distribution does not seem to be associated with climatic changes.

Thus the late Quaternary is seen to have been host to some large changes in the geographical distributions of many land snails along the north coast of Jamaica. As in the temperate zone during that time, there was no shifting of faunas *en mass* but instead, different species were affected in different ways.

ABSTRACTS
POSTER SESSION

Arranged by Clement Lee Counts, III
University of Delaware

CHRONOLOGY OF THE INVASION OF NORTH AMERICA BY *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE). Clement L. Counts, III, College of Marine Studies, University of Delaware, Lewes.

Zoogeographic records of the exotic Asiatic clam *Corbicula fluminea* (Müller, 1774), from the malacological collections of twenty-three museums in the United States, were examined with respect to localities of occurrence and dates of collection. Similar information was gathered from state natural resources departments and published accounts of *C. fluminea* in the United States. All data were combined and then segregated into yearly summaries. Zoogeographic distribution maps were plotted for *C. fluminea* for the time intervals ca. 1925-1945, 1946-1955, 1956-1960, 1961-1965, 1966-1970, 1971-1975, 1976-1982. The zoogeography of *C. fluminea* in the United States through time is related to human transport and theories of animal transport do not account for its present or historic distribution.

ONTOGENETIC SHELL AND RADULAR CHANGES IN THE DENTALIID SCAPHOPOD, *GRAPTACME CALAMUS* (DALL, 1899). Paul S. Mikkelsen, Harbor Branch Foundation, Inc. Ft. Pierce, and **Kathryn Muldoon-McLaughlin,** Applied Biology, Inc., Jensen Beach, Florida.

Specimens of *Graptacme calamus* (Dall, 1899), collected from offshore of the central east coast of Florida, were examined for details concerning ontogenetic changes in shell length, diameter, sculpture and fractionation. Although the species is known to form an apical plug following breakage of the shell, specimens were determined to fracture at particular, possibly predetermined points, at regular intervals. Shell sculpture changed from smooth to minutely ribbed at a length of about 1.5 mm. The rachidian tooth of juveniles possesses a central prominence which flattens and broadens with age of the specimen, to attain the flat appearance characteristic of the adult rachidian. The number of radular rows increased ontogenetically.

ABSTRACTS
SHELL MICROSTRUCTURE
SYMPOSIUM

Arranged by Robert S. Prezant
University of Southern Mississippi

SHELL MICROSTRUCTURE AND MINERALOGY OF TWO SPECIES OF BIVALVES FROM DEEP-SEA HYDROTHERMAL VENTS. **Richard A. Lutz,** Rutgers University, New Jersey.

The mineralogies and microstructures encountered within the shells of the two species of bivalves found to date at deep-sea hydrothermal vents along the Galapagos Rift and at sites located along the East Pacific Rise are typical of calcified structures encountered within their respective families (Vesicomyidae and Mytilidae). The shell of the large, white vesicomyid (*Calyptogena magnifica*) is entirely aragonitic. Four major shell layers have been recognized in this clam and may be classified, from the often-corroded shell exterior inwards, as: 1) homogeneous; 2) predominantly fine complex crossed lamellar with patches of irregular complex crossed lamellar; 3) irregular prismatic (pallial myostracum); and 4) cone complex crossed lamellar. The calcified layers of the presently unclassified mytilid from both the Galapagos Rift site and the recently-discovered vent fields at 13°N consist, from the vacuolated periostracum inwards, of: 1) fibrous prismatic calcite; 2) nacre (aragonite); 3) irregular prismatic aragonite (pallial myostracum); and 4) nacre (aragonite).

All examined specimens of both species were sampled from depths between 2000 and 3000 m. Such depths are well above reported calcite compensation depths in these eastern Pacific regions but substantially below the reported calcium carbonate compensation depths for aragonite in these areas. While the thin veneer of calcite and the relatively thick organic periostracum appear to effectively prevent substantial dissolution of the relatively thin and fragile shell of the mytilid throughout its life, no such protection is afforded by the aragonite of the outer shell of the vesicomyid. It is suggested that extremely rapid shell deposition must be occurring throughout the life of the clam in order to "offset" destructive dissolution processes.

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DAHLLITE IN THE PERIOSTRACUM OF *LITHOPHAGA NIGRA* (MOLLUSCA: BIVALVIA) AND ITS TAXONOMIC AND FUNCTIONAL IMPLICATIONS. **Thomas R. Waller,** Department of Paleobiology, Smithsonian Institution, Washington, D.C.

The outer side of the dark brown periostracum of the non-incrusted boring mussel, *Lithophaga nigra* (Orbigny), turns chalky white in bleach (2% NaOCl) and leaves a bleach-insoluble residue. Scanning electron microscopy (SEM) of bleached and unbleached periostracum revealed a distinctive mineralized outer layer packed with columnar hexagonal crystals with flat ends. The crystals, which reach 0.8 μm in length and 0.2 μm in diameter, are calcium hydroxyl-apatite with an X-ray diffraction pattern like that of dahllite as reported by Watabe (1956: *Science,* 124) in the prodissoconch I of *Pinctada martensi* (Dunker). The mineralized layer of *Lithophaga nigra* is underlain by typical unmineralized periostracum, and both the mineralized and unmineralized layers originate in the periostracal groove of the mantle.

Bleach tests and SEM showed that a nearly identical mineralized outer layer is also present in the periostracum of other non-incrusted species of *Lithophaga* but is absent in the periostracum of species covered by calcareous (calcitic and/or aragonitic) incrustations. Calcareous incrustations and the mineralized outer periostracal layer are not homologous, because the former do not originate in the periostracal groove but rather are secondary deposits formed within mucus on top of the fully formed periostracum.

Wilson (1979: *Records of the Australian Museum,* 32) found several major anatomical differences between incrusted and non-incrusted *Lithophaga* in Queensland and suggested that if further studies of additional species sustain the intergroup differences, two genera should be recognized. The available names would be *Lithophaga* Röding, 1798, for the non-incrusted group and *Leiosolenus* Carpenter, 1856, for the incrusted group. The differences in periostracal structure between the two groups reported here give further support for this generic level separation. Incrustations and phosphatized periostracum may represent two independent adaptations to life in chemically excavated boreholes. In non-incrusted *Lithophaga,* dahllite may harden the periostracum and protect it against abrasion as the bivalve moves within its borehole. Thick calcareous incrustations may serve the same purpose, but in addition they strengthen and protect the exposed posterior end of the shell.

MICROSTRUCTURE OF THE CALCIFIED BYSSUS OF *ANOMIA SIMPLEX.* **Robert S. Prezant,** University of Southern Mississippi, Hattiesburg.

The calcified byssus of the common jingle shell *Ano-*

mia simplex offers a unique and easily accessible structure for the study of calcification and mineralization in molluscs. The rigid byssal attachment system of the anomiids is composed of a slightly recurved, elongated pillar that extends from a modified foot through a byssal notch in the right valve to a flared attachment plaque. The upper portion of the byssus, otherwise enclosed by a basal, cup-shaped portion of the foot, consists of a series of parallel lamellae that run along the long axis of the byssus. These calcified lamellae are produced within a series of secretory folds or leaflets composing the cup-shaped pedal region. Each lamella is formed within a single fold. Lamellae terminate near the base of the byssus and gradually conform to a relatively smooth plaque sector. The basal plaque, superficially smooth with only small pores and infrequent pitting disturbing this smoothness, gradually spreads over and is firmly attached to the substratum. The plaque has similar microstructural qualities as the lamellae but not in the form of distinct sheets. The external microstructure of both often appears as a series of spindle shaped granules lying obliquely to the byssal long axis. These spindle shaped packets are reminiscent of similar structures found in other, relatively simple calcified systems and may be revealing a consistent and widespread means of inorganic deposition.

THE MICROSTRUCTURE OF NORMAL AND REGENERATED SHELL IN *TEGULA* (ARCHAEOGASTROPODA). Charlene Reed-Miller, Florida State University, Tallahassee.

Shells from five species of the marine snail *Tegula* were examined by scanning electron microscope to determine the ultrastructure and orientation of shell layers. Four shell layers were identified, each with some variation in the microstructure among the species of snails. Shell regeneration was initiated by cutting a $4mm^2$ window in the first body whorl of the snails. The regenerated shell was observed by scanning electron microscopy and energy dispersive X-ray analysis. Newly regenerated shell appeared as small (1 μm) doubly-pointed crystallites. These crystallites increased in size and coalesced until a thin, layered sheet of calcium carbonate filled the window, approximately 35 days after shell injury. There is a great dissimilarity in the microarchitecture between normal and regenerated shell in *Tegula*. The differences in crystal type are probably correlated with the rate of shell deposition. Supported by grant No. DE05491 from the National Institute of Health.

X-RAY MICROANALYSIS OF OYSTER MANTLE: CALCIUM TRANSPORT. Lyle Walsh, Department of Physiology, University of California, Los Angeles.

The shell of molluscs is made by the outer epithelium of the mantle. These cells secrete and modify the extrapallial fluid from which shell matrix and mineral are formed. Constituents of the extrapallial fluid are regulated by mantle transport processes.

Mantle from the American oyster *Crassostrea virginica* was quench frozen, freeze substituted and embedded in resin. One micron thick sections were cut and etched. Subcellular regions were localized and analyzed by x-ray microanalysis.

The results indicate: 1) Na and Cl are removed from the cell 2) K, Mg, and Zn are concentrated from seawater 3) S and P are accumulated 4) Ca is located uniformly over most of the cell 5) Ca is concentrated along the microvilli and 6) no Ca granules occur in the mantle.

Several theories of trans-epithelial Ca transport can be ruled out. Electro-chemical diffusion cannot lead to extrapallial Ca accumulation because the sustaining potential would be shunted to seawater. Ion selective intercellular junctions would not provide a transport pathway because no increase of Ca was found in the intercellular spaces. Since mitochondria did not accumulate Ca, Lehninger's model of Ca transport is ruled out.

Ca transport across outer mantle epithelium is restricted to 1) Na/Ca exchange 2) Ca-ATPase pump 3) secretion of proteins with bound Ca; all across the apical membrane. Ca accumulations along the microvilli may be precipitate on newly formed matrix nucleation sites.

HETEROGENEOUS DISTRIBUTION OF TRACE AND MINOR ELEMENTS IN SHELL OF THE OYSTER, AN HYPOTHESIS. Melbourne R. Carriker, College of Marine Studies, University of Delaware, Lewes, **Charles P. Swann,** Bartol Research Foundation of the Franklin Institute, University of Delaware, Newark, and **Robert S. Prezant,** Department of Biology, University of Southern Mississippi, Hattiesburg.

The distribution of 16 elements studied by us in valves of *Crassostrea virginica* with a proton microprobe is conspicuously heterogeneous, not only within one but also among different mineralogical types of shell, confirming observations by Immega (1976) with AAS in the valves of *C. gigas* and *Ostrea lurida*. He suggested that many elements present in valves come from particles of "contaminated" inorganic detritus incorporated in the shell at the mantle edge during shell formation. Our study of the activity of the part of the living mantle ventral to the adductor muscle, and scanning electon microscopy of prismatic shell formation at the periphery of the valves in *C. virginica* support Immega's suggestion. Mantle lobes ventral to the adductor muscle are muscularly active and highly contractile, so that not only mantle margins but also extrapallial surfaces of the mantle epithelium are exposed to particles suspended in seawater. Furthermore the organic film (that precedes shell formation) secreted by the mantle edge appears highly viscid and probably readily adsorbs microscopic particles suspended in seawater circulated through the mantle cavity.

ABSTRACTS
SECOND INTERNATION SYMPOSIUM
ON MOLLUSCAN GENETICS

Arranged by George M. Davis
Academy of Natural Sciences
of Philadelphia

HABITAT STABILITY, POPULATION HISTORIES AND PATTERNS OF VARIATION IN *CEPAEA.* Robert Cameron, Birmingham University, and Patrick Dillon, Bulmershe College, Reading, United Kingdom.

Recently, it has been suggested that patterns of variation in *Cepaea* populations relate to habitat stability and population history, and in particular that the microgeographical variation known as area effects are associated with habitat instability and population bottlenecks.

In this study, two districts in Wiltshire, England, with well known landscape history were sampled after predictions were made of the types of variation to be found.

These predictions are substantially confirmed. Both districts contain areas of stable and unstable habitat. In stable areas *Cepaea* shows variation with habitat, of a type suggesting visual selection for crypsis. Less stable areas also show this variation, but to a lesser extent, and involving fewer loci. They also show area effects.

Spatial correlations in morph frequencies are generally much stronger in unstable areas than the stable ones, indicating stronger geographical patterns. The extent to which populations of *Cepaea* which have colonized new woods match their habitat is dependent on distance from the nearest ancient woodland.

These results strengthen the hypothesis that founder effect and other aspects of population history have an important role in determining the patterns of variation seen in many population of *Cepaea.*

THE EFFECT OF DENSITY AND SHELL PHENOTYPE ON JUVENILE GROWTH AND ADULT FECUNDITY OF *CEPAEA NEMORALIS* (L) (GASTROPODA: PULMONATA). M. A. Carter and M. Ashdown, Portsmouth Polytechnic, United Kingdom.

The polymorphic landsnail *Cepaea nemoralis* (L) is widespread on the chalk grassland of a particular dry valley system on the South Downs near Portsmouth, UK. The populations, which are continuous within an area 1 km square, have been studied over a fourteen year period. Two sets of shell characters vary in these populations. (i) Over several of them, shell size shows clinal variation but this character has also been found to vary within a population with time. Mark-release-recapture experiments have shown that shell size is inversely proportional to density. Laboratory experiments have shown that increased density reduces juvenile activity and growth. Reduced adult size decreases fecundity as does increased density during the egg-laying period. (ii) Shell colour and banding pattern frequencies have been shown to be constant within populations over twelve years. There are clinal variations between populations for these characters. The patterns of variation are related in part to the shell size distributions.

Two experiments were set up during 1981 to investigate any possible differential effect of density on growth and fecundity of snails with different shell colour phenotypes. Juvenile pink and yellow banded snails showed differential activity and growth in response to different densities in the laboratory. Adults of these phenotypes were maintained at three densities and various fecundity components were measured. There were differences between the pinks and the yellows but they were not related to density.

A TRANSPLANTATION EXPERIMENT ON TWO SPECIES OF HELICID SNAILS IN NORTHWEST SCOTLAND. Jeremy J. D. Greenwood, Department of Biological Sciences, The University, Dundee, Scotland, and David T. Parkin, Department of Genetics, University Park, Nottingham, England.

The object of this experiment was to discover whether, when snails are reciprocally transplanted between sites differing in morph-frequencies, the morphs that are naturally less common at each site suffer higher mortality than those naturally more common.

Cepaea hortensis and *Arianta arbustorum* were collected at two sites in N.W. Scotland. The sites differed in proportion of the two species and in morph-frequencies. The snails were marked. Half were replaced in their site of origin and half transplanted to the other site. Collections made a year later indicated differences both between and within species in mortality and activity patterns. The within-species differences comprised both differences between morphs and between snails from different sites. In addition, mortality was consistently higher at one site, for both native and transplanted snails.

COILING IN *PARTULA:* THE EVOLUTION OF AN ISOLAT-

ING MECHANISM. Bryan Clarke, University of Nottingham, England and **James Murray,** University of Virginia, Charlottesville.

On the island of Moorea in French Polynesia, *Partula suturalis* varies in the coil of its shell. In the northern parts of the island it is sinistral, and in the southern parts dextral. Between the two zones there is a region of transition where populations are polymorphic for coil. It seems that the southern populations of *P. suturalis* have become dextral as a consequence of interactions with a coexisting sinistral species, *Partula mooreana.* In *P. suturalis* the coil of the shell is determined by the genotype of the mother, and sinistral is dominant to dextral. Because *Partula* are crossfertilizing ovoviviparous hermaphrodites, we can dissect the snails and observe the coils of their young. This allows us to estimate, in polymorphic populations, the degree of isolation between shells of different coil, by testing how the frequencies of mother-child combinations depart from those expected under random mating.

MOVEMENT AND GENE FLOW IN *PARTULA TAENIATA.*

James Murray, University of Virginia, Charlottesville.

The land snail *Partula taeniata* is the most abundant and widespread member of this genus inhabiting the island of Moorea in French Polynesia. Local populations are differentiated with respect to size and shape of the shell and frequencies of the genes controlling color and banding of the shell. In order to determine the amount of gene exchange between populations, two experiments were performed. In the first, a 10 × 10 m square was divided into 25 quadrats and the snails were marked to indicate their initial locations. Movements were recorded over a period of nine weeks, with a subsequent collection after five years. The mean radius of individual movements rose to 219 cm over the initial period, with a variance increasing faster than the mean. The maximum recorded displacement was 737 cm. Recaptures after five years establish longevity in nature and show that individuals may remain for long periods close to their initial points of capture.

In the second experiment, genetically marked individuals were introduced at one place into a natural population. Samples taken after one year and ten years show that the introduction was sucessful and that the genes have spread from the point of introduction. After ten years no marked animals remained in the population, but the mean displacement of the introduced genes had risen to 1059 cm with a maximum recorded distance of 27 m.

SHELL COLOURS OF LANDSNAILS IN THE NEGEV DESERT, AND THE IMPORTANCE OF RODENT DISTRIBUTION.

Joseph Heller, The Hebrew University, Jerusalem, Israel.

White shells are associated with exposed habitat, since they reflect more radiation than dark ones do. Since deserts are exposed to severe solar radiation, one might expect to find a predominance of white snails in them. In contrast to this expectation, 20 out of 23 species in the Negev Desert are not white. Amongst polymorphic desert species, there is no north-to-south cline corresponding to the north-to-south increase in aridity. White snails in the desert thus do occur occasionally, but as an exception, not as a rule. Apparently even in the Negev, where solar radiation is exceptionally high, selective forces for anti-radiation devices can be overridden by other, greater selective forces. One such force is predation. Evidence for the importance of microdistribution of predators in determining shell colours comes from the Caesana sand dunes (in a Mediterranean landscape). Here in contrast to our expectations, effectively banded (and cryptic) shells of *Theba pisana* are found at a high frequency in habitats sparsely covered by vegetation; at an intermediate frequency in moderately covered habitats; and are practically absent from densely covered ones. Noteworthy, this is almost precisely the relative abundance of gerbils in this area also. This parallelism strongly suggests that it is indeed this variation in the intensity of predation pressure that directly causes the variation in the distribution of the morphs. The Negev Desert is indeed a very exposed habitat; but it is also densely populated by rodents, many of which eat snails to balance their water requirements, thus selecting against the white, conspicuous shells. Hence few white shells are found in deserts.

ECOGENETICS OF *THEBA PISANA* (MÜLLER) (PULMONATA: HELICIDAE) AT THE EDGE OF ITS RANGE.

Robert H. Cowie, Zoology Department, University of Liverpool, Liverpool, United Kingdom.

The highly variable coastal Mediterranean land snail *Theba pisana* reaches the northern limit of its range at a small number of localities in the southern and western parts of the British Isles, where its local distribution emphasizes the importance of climatic factors. At Tenby (South Wales) the life-cycle is biennial, not annual, in response to the relatively short growing season, and shells have a generally darker appearance than in Mediterranean localities. Studies of population structure and effective population size have shown that the occurrence of genetic drift cannot be discounted here. Variation in shell banding pattern at Tenby has been broadly characterised genetically by breeding experiments. Three loci (at least) have been inferred with two alleles showing dominance at each. Epistasy allows only four main phenotypes to appear: plain unbanded, dotty unbanded, dark five-banded, yellow five-banded. The determination of these morphs has allowed the variation in the field at Tenby to be quantified. Morph frequencies differ at the different sites, but appear fairly constant over five years. Banded snails may be at an advantage during at least the second year of the life-cycle. The selective agent cannot be identified, but drift is unable to account for the trend. Brief comparisons of this polymorphism with that exhibited elsewhere suggest three geographical regions (Britain, northern France, the Mediterranean), each with a different complex of morphs.

GENETICS OF SOME MORPHS IN THE LAND SNAIL

***THEBA PISANA.* Arthur J. Cain,** Zoology Department, University of Liverpool, United Kingdom.

The exceptionally variable snail *Theba pisana* is abundant in Mediterranean and west European juxta-littoral habitats, and has been introduced elsewhere. So far, the banding variation has defied description and analysis; basically it has five bands as in other helicids. A breeding program over several years allows a number of morphs to be characterized, including unbanded forms with band three enhanced, others with it reduced, some with an additional line of dots at the lowest level of band three, and fully five-banded. A hyalozonate and subhyalozonate form are also described. There can be considerable variation in the expression of most morphs, caused at least in part by genetic modifiers, so that, unlike in *Cepaea,* random samples often show apparently continuous variation. This explains the difficulty previous workers have had in scoring morphs. It is suggested that indistinct morphs provide a continuum of variation, so that predators are more likely to be confused than if they memorize a few well defined forms.

SPECIES COHESIVENESS AND GENETIC CONTROL OF SHELL COLOR AND FORM IN *THAIS EMARGINATA* (PROSOBRANCHIA: MURICACEA). A. Richard Palmer,

Department of Zoology, University of Alberta, Edmonton.

Thais (=Nucella) emarginata has one of the largest geographical ranges of rocky-intertidal, prosobranch gastropods of the northeastern Pacific. It extends from the Bering Sea through southern California and has been reported into Mexico, a latitudinal range of nearly 35 degrees. Of 91 intertidal species, only three have ranges as great or greater (average for all species, 21.2±9.61 deg, N=91; neogastropods only, 20.8±8.42 deg). *T. emarginata* has direct development from benthic egg capsules with no pelagic larvae, and throughout its latitudinal range it is restricted to the mid- and upper-intertidal of rocky shores (+1m above MLLW or higher). It is also generally restricted to areas with intermediate to high wave exposure or moderate currents. Consequently expanses of deep water, sand beaches and quiet estuaries or inlets all act as barriers to gene flow. In addition, lateral movements along rocky shores are not very great; during summer months marked individuals moved less than 2m/mo, and over a twelve month period net displacement averaged approximately 5 m.

Pairwise crosses of *T. emarginata* from populations of southeast Alaska (USA) and Vancouver Island (Canada) revealed that in spite of very restricted gene flow, individuals from these distant populations (circa 1500 km) were capable of producing F1 offspring which grew to adult size successfully. Rate of genetic divergence thus appears to be low in this species. Females from Alaska produced consistently fewer egg capsules in the lab than those from Vancouver Island, but there were no differences between within- or between-population crosses.

T. emarginata also exhibits variation in shell color, banding and sculpture. Shell-morph frequencies of F1 offspring suggest that: 1) the color black is dominant over orange and white, 2) banding is recessive to lack of banding, and 3) the capacity to produce spiral sculpture may be controlled by a single gene or a block of tightly linked genes.

WHAT SHALL I MEASURE ON MY SNAILS? ALLOZYME DATA AND MULTIVARIATE ANALYSIS USED TO EVALUATE THE GENETIC COMPONENT OF MORPHOLOGICAL VARIABLES IN *GONIOBASIS PROXIMA.* Robert T. Dillon, Jr.,

Academy of Natural Sciences, Philadelphia, Pennsylvania.

The pleurocerid snail *Goniobasis proxima* inhabits small streams in the piedmont and mountains of the southern Appalachians. In a recent study of electro-phoretically detectable variation at 15 enzyme loci, Dillon and Davis (1980) distinguished three races of *G. proxima.* In the present work, I took 33 measurements and six counts on ten snails from each of these three races using standardized techniques. These variables were screened by requiring that they vary at the 99% confidence level among the three races. Multivariate analysis of variance showed that 12 of the 33 measurements did not vary significantly among races, and nonparametric statistics eliminated four of the six counts.

The remaining 21 measurements and two counts were then taken on 10 individuals from each of 22 more *G. proxima* populations. Principal component analyses were performed on both the correlation and covariance matrices of the 21 measurement variables calculated over all 250 individual snails. The first principal component, representing size variance, was disregarded, and the 21 measurements were ranked by their contributions to the variance on the significant principal components remaining. If growth is modelled using covariance, the 13 hard-part measurements seem to have more genetic component than the 20 soft-part measurements. Measurements of the shell and external head seem to be more valuable than measurements on the body and central nervous system, with trophic apparatus measurements falling in between. If growth is modelled using correlation, no difference is apparent between hard and soft-part measurements. Measurements on the external head, central nervous system, and trophic apparatus seem to have more genetic component than shell or body measurement.

Despite these differences, overall morphological population divergence estimated using the corrrelation assumption gives results similar to those obtained if morphological divergence is estimated with the covariance assumption. Such population divergence measurements are correlated both with geographic distance and environmental difference between populations.

KARYOTYPES OF SOME OSTREIDAE AND MYTILIDAE (BIVALVIA). Catherine Thiriot-Quiévreux,

Station Zoologique, Villefranche-sur-mer, France.

The chromosomes of some Bivalvia, *Ostrea edulis, Crassostrea gigas, Mytilus edulis, Mytilus galloprovincialis* and *Mytilus desolationis,* were obtained from mitotic metaphases of branchial tissue with cellular suspension technique. The karyotypes were established according to the length of the chromosome and the position of the centromere. The occurrence of metacentric, submetacentric and telocentric chromosomes in *Ostrea edulis* (2n=20) as well as the difference of size between the pair n°1 and the pair n°10 emphasize the cytological interest of this species compared to *Crassostrea gigas* (2n=20), which show only metacentric and submetacentric chromosomes. In all three species of *Mytilus* (2n=28), metacentric, submetacentric and telocentric chromosomes occur. Pair n°2 appears to be metacentric in *Mytilus edulis* and telocentric in *Mytilus galloprovincialis* confirming the separation between these two species.

CYTOGENETIC ANALYSIS OF INTERSPECIES HYBRIDS OF *ASHMUNELLA* (MOLLUSCA: PULMONATA: POLYGYRIDAE) IN THE LIGHT OF STANDARD AND C-BANDING TECHNIQUES. Noorullah Babrakzai, Department of Biology, Central Missouri State University, Warrensburg and **Walter B. Miller,** Department of General Biology, University of Arizona, Tucson.

Twenty interspecies hybrids of *Ashmunella proxima albicauda* Pilsbry and Ferriss X *A. lenticula* Gregg were reared in terraria under laboratory conditions. After reaching maturity the ovotestes of the hybrids were examined cytologically. The hybrids are intermediate in shell morphology. Karyotypes of the parental species were constructed from developing embryos of the parental species populations. *A. proxima albicauda* has four distinct chromosomes with large C-band positive heterochromatic long arms in the mitotic metaphase. Such chromosome markers are absent in the *A. lenticula* karyotype. The hybrids have half of the *A. proxima* chromosome markers in both meiosis and mitosis. The meiotic behavior of chromosomes in hybrids ranged from complete synapsis to signs of asynapsis in pachytene. Univalent, multivalent formation, evidence of translocations, inversions, stickiness of meiotic chromosomes, were observed in all stages of the meiosis. We summarize our conclusions as follows: 1) *A. proxima* and *A. lenticula* are two closely related but cytologically and genetically different species; 2) We hypothesize that the intermediate nature of the hybrid shell phenotype is due to expression of a gene or genes, one half of whose alleles are contributed by each parental species genome; 3) The karyotypes of the two species have evolved in different directions; 4) The observed cytological differences in karyotypes of the two species represent a gross oversimplification of their genetic differences; 5) Exercising conservatism in synonymizing land snails species of the arid Southwest is strongly recommended.

INFLUENCE OF SNAIL AGE ON GENETIC VARIATIONS IN SUSCEPTIBILITY OF *BIOMPHALARIA GLABRATA* FOR INFECTION WITH *SCHISTOSOMA MANSONI.* Charles S. Richards, Biomedical Research Institute, Rockville, Maryland.

Four patterns of susceptibility in *Biomphalaria glabrata* for infection with *Schistosoma mansoni* have been demonstrated: **I,** nonsusceptible at any age; **II,** juvenile susceptible/adult nonsusceptible; **III,** susceptible at any age; **IV,** juvenile susceptible/adult variable. Crosses between **II** and **III** showed that adult susceptibility was determined at a single gene locus with nonsusceptibility dominant. Crosses between **III** and **IV** suggested the latter carried the recessive alleles for susceptibility, but another factor modified expression so that some snails became nonsusceptible. Most of the type **IV** snails nonsusceptible as young adults reverted to susceptibility in old age. Some snail stocks susceptible to Puerto Rican PR-1 *S. mansoni* at any age are juvenile susceptible/adult nonsusceptible to Puerto Rican *S. mansoni* PR-2. Crosses suggest a third allele is involved. Crosses also suggest some snails nonsusceptible at any age carry unexpressed the alleles for adult susceptibility.

Five Puerto Rican *B. glabrata* stocks have been exposed to 13 genetically different Puerto Rican *S. mansoni* strains. One snail stock tests susceptible to all the strains at any age. Three snail stocks test juvenile susceptible to all the parasite strains, but show differences in adult susceptibility. Some stocks show adult variability. One stock is nonsusceptible to some strains, juvenile susceptible to others, and is adult nonsusceptible to some of the latter.

These studies suggest the occurrence of snail populations juvenile susceptible/adult nonsusceptible to endemic parasite strains is not uncommon. Juvenile snails can probably serve as adequate intermediate hosts to maintain transmission. It is important, therefore, in monitoring field snail populations for infection or testing for susceptibility to include juvenile as well as adult snails.

CHROMOSOMAL EVOLUTION IN SNAILS OF THE GENERA *BULINUS* AND *BIOMPHALARIA.* Michael A. Goldman, Medical Genetics Section, Baylor College of Medicine, Houston, Texas, **Philip T. Loverde,** Department of Microbiology, State University of New York, Buffalo, **C. Larry Chrisman,** Department of Animal Sciences, Purdue University, W. Lafayette, Indiana, and **Dee A. Franklin,** Texas A&M University, College Station.

The planorbid snail genera *Bulinus* and *Biomphalaria,* have presented the systematist with problems of critical interest. The basic chromosome number for the family Planorbidae is $2n=2x=36$, but species of *Bulinus* have been shown to exhibit four levels of ploidy—diploid, tetraploid, hexaploid, and octoploid. In contrast, none of the many populations of *Biomphalaria* that have been studied cytologically in this and in previous reports contain other than the basic diploid chromosome number.

In the present paper, we review the data on karyotypic evolution in *Bulinus* and *Biomphalaria,* and data relevant to a description of the breeding biology of these two groups. We then discuss the possibility of a connection between breeding biology and chromosomal evolution in *Bulinus* and *Biomphalaria,* in order to assess the validity and applicability of models that propose a connection between inbreeding or low effective population size and rapid rates of chromosomal evolution.

Our data revealed that *Biomphalaria* is karyotypically more conservative than *Bulinus* at the diploid level. While many species of *Bulinus* differ in karyotype, *Biomphalaria* species are not distinguishable on the basis of karyotype analysis. We studied G-banded karyotypes of four populations of *Biomphalaria glabrata* and one of *B. straminea, Bulinus tropicus, B. natalensis, B. truncatus* and *B.* sp. ($2n=36$) from Mazoe Dam, Zimbabwe. In considering these data, and data on nine species published by previous workers, we observed from 14 to 16 metacentric pairs in all *Biomphalaria* species studied, while the corresponding range for *Bulinus* was from 8 to 17.

We hypothesize that the contrasting rates of chromosome evolution between *Bulinus* and *Biomphalaria* is a result of *Bulinus* having small effective population size as compared with *Biomphalaria.*

POPULATION STUDIES ON *BULINUS CERNICUS* FROM MAURITIUS. D. Rollinson and **C. A. Wright,** British Museum (Natural History), London.

Bulinus cernicus occurs commonly in a variety of habitats in the low lying areas of Mauritius where it serves as the intermediate host for the trematode *Schistosoma haematobium.* For the most part the snail habitats are well isolated from each other and gene flow between the snail populations must presumably be at a very low rate. The morphological diversity within *B. cernicus* is such that recent investigators have suggested that more than one species of *Bulinus* may be present on the island. The present study was undertaken to gain a better understanding of the variation and populations structure of this planorbid.

Snails have been examined from a majority of the known habitats. Although preliminary observations on water chemistry of the different sites revealed a marked correlation between the shell form and composition of the water, quite striking differences in the shells, radular teeth and growth rates persisted within the laboratory stocks. All populations tested proved susceptible to local isolates of *S. haematobium* and to certain other African schistosomes not associated with Mauritius. Electrophoresis of enzymes by isoelectric focusing showed regional differences in gene frequency and a high level of heterogeneity within *B. cernicus* in comparison to other species within the *B. forskali* group. Laboratory mating experiments did not indicate any apparent reproductive isolation between representatives of distinct populations and the progeny from such crosses were fertile. Although, when isolated, snails would self-fertilize, investigations utilising enzyme markers showed a marked preference for cross-fertilization and that donated sperm could be stored for several weeks. Many of the habitats of *B. cernicus* are subject to drought and/or flooding, the ability to store sperm might help preserve genetic variability when the survival of the population depends upon a few snails.

GENETIC DIFFERENTIATION AMONG *BIOMPHALARIA*. Margaret Mulvey, Savannah River Ecology Laboratory, South Carolina and **Robert C. Vrijenhoek,** Rutgers University, New Jersey.

Electrophoretic techniques have been developed for multilocus genetic screening of snails of the genus *Biomphalaria.* The genetic basis for eleven of these electrophoretic phenotypes has been demonstrated through controlled crosses. These loci plus a locus controlling body pigmentation apparently mark eight linkage groups in *B. glabrata.* Use of these markers has provided information regarding genetic divergence among strains and species of *Biomphalaria.* Reproductive incompatibilities were observed during mating experiments with some laboratory strains of *B. glabrata* This was especially marked in crosses involving an N.I.H. albino strain and a strain originating from the Dominican Republic. An estimate of genetic distance (Nei, 1972), based on electrophoretic markers of 0.32, was obtained for the albino and Dominican Republic strains. This distance is comparable to those observed at the species level of *Drosophila.* Populations of *B. glabrata* from Puerto Rico and *B. alexandrina* from Egypt have been examined for evidence of population subdivision and inbreeding. There was little evidence of inbreeding within local populations but strong differentiation among local populations. This differentiation has been attributed to low effective migration rates and restricted gene flow among local demes.

GENETICS OF THE CLAM *MERCENARIA MERCENARIA*. II. SIZE AND GENOTYPE. Laura Adamkewicz, Stephan R. Taub, and **J. R. Wall,** George Mason University, Fairfax, Virginia.

This paper reports on the relationships between allozyme genotypes at five loci and shell size at the age of one year in clams bred and reared under hatchery conditions. Clams of known genotype, from a wild population of known composition, were individually induced to spawn. All gametes were mixed at one time to produce a randomly bred cohort of clams. After one year a sample of 1081 were measured and their enzyme phenotypes determined by a starch gel electrophoresis for *Pgd, Lap, Pgi, Pgm-2* and *Pgm-3.* The cohort's genotype frequencies differed significantly from Hardy-Weinberg expectation for all genes except *Pgd,* but only for *Lap* was the deviation associated with heterozygosity, for which there was a striking deficiency. Since the cohort was randomly bred, the Wahlund effect cannot explain this observation while differential survival can. The joint frequencies by pairs for three loci (*Lap, Pgm-3, Pgi*) were not in linkage equilibrium. Because the three loci assort independently in Mendelian crosses, this effect is most likely the result of differential survival. Two genes, *Lap* and *Pgm-3*, show highly significant associations of genotype with shell size. In the case of *Pgm-3*, the data fit a model of additive allele effects with no interaction. For *Lap,* allelic interactions do occur in certain genotypes. In neither instance is there a specific effect of heterozygosity *per se.*

POPULATION ECOLOGY OF *CEPAEA NEMORALIS* AND *C. VINDOBONENSIS* ALONG THE NORTHERN ADRIATIC COASTS OF ITALY. Cesare F. Sacchi, Istituto di Ecologia Animale ed Etologia, Università di Pavia, Italy.

There are sparse and discontinuous populations of *C.*

nemoralis nemoralis along the northern Adriatic coasts of Italy between Ravenna and Monfalcone, and of *C. vindobonensis* from the mouth of the river Tagliamento to Monfalcone.

Typically, both species live on the sand dunes that lie between the sea and the lagoons or recently thermophilous biotopes, and were originally consolidated by *Quercus ilex*, which is now often replaced by pinewood plantations, mainly of *Pinus pinea*.

In this woodland habitat *C. nemoralis* is mainly represented by the 12345 morph, with the bands seldom fused. Pink shells are more frequent towards the north, along the Friuli coast, where there is also a richer shell-banding polymorphism. Albinos are rare, and both interrupted ("dotted") and pale ("smudged") bands are not common, as compared with sharply defined and continuous bands.

Average shell increases slightly towards the south, where the climate is dryer and less "oceanic", with more variation between summer and winter, and where the lime content of the soil is reduced.

In *C. vindobonensis,* pale-banded shells, and shells with pale peristome lips, are rare, but they seem to occur in particularly dry habitats.

Predation never plays an important role.

GENETIC DIFFERENTIATION AND POPULATION STRUCTURE OF THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* IN THE CHESAPEAKE BAY. Norman E. Buroker, Rutgers University, Piscataway, New Jersey.

The American oyster was studied by horizontal protein electrophoresis with relation to levels of genetic variation and differentiation among ten oyster bars in the Chesapeake Bay. The observed heterozygosities ranged form 0.196 to 0.230 while the proportion of polymorphic structural loci ranged from 0.448 to 0.531 among demes. The genetic similarities among oyster bars was, on the average, 99%, suggesting little genetic differentiation. However, F_{st} statistics revealed that 23 of 41 alleles displayed statistical significance among demes indicating spatial heterogeneity among oyster bars within the Chesapeake Bay. Principal component and stepwise multivariate analyses of 28 common alleles indicate that the ten oyster bars can be partitioned into four different latitudinal groups (subpopulations) in the Chesapeake Bay. It is suggested that the four subpopulations are maintained by a balance between the migration of planktonic oyster larvae and the adaptation of genotypes to local environmental conditions.

GENETIC DIVERSITY WITHIN AND BETWEEN POPULATIONS OF AMERICAN OYSTERS (*CRASSOSTREA*). Dennis Hedgecock, Bodega Marine Laboratory, University of California, Bodega Bay.

American oysters of the genus *Crassostrea* form a complex of closely related populations having extremely broad distributions and uncertain systematic affinities. *C. virginica* and *C. rhizophorae* are believed to intergrade in Central America south of the Yucatan Peninsula and on the basis of hybridization studies have been considered subspecies. *C. corteziensis* is thought to have diverged in the Pacific Ocean from a *C. virginica* ancestor isolated by the rise of the Central American land bridge.

Electrophoretic studies have been made of a total of eight populations and 400 individuals to determine the amount of genetic diversity within and between populations and taxa. Average heterozygosities ($\bar{H}$), proportions of polymorphic loci (P), and numbers of loci studied are as follows: $\bar{H} = 0.19$, $P = 0.73$, 22 loci for *C. virginica;* $\bar{H} = 0.14$, $P = 0.62$, 16 loci for *C. rhizophorae;* and $\bar{H} = 0.15$, $P = 0.63$, 16 loci for *C. corteziensis.* Excesses of homozygous genotypes over Hardy-Weinberg (random mating) expected proportions within populations are common. Average genetic distance among conspecific populations is about 0.1 while among species it is 0.6 indicating that these three taxa are well separated. *C. corteziensis* appears to be slightly closer to *C. virginica* than to *C. rhizophorae* at the protein level, but attempts to hybridize the former two species have thus far been unsuccessful (R. W. Menzel, personal communication).

THE SYSTEMATIC STATUS OF *MYTILUS GALLOPROVINCIALIS* IN WESTERN EUROPE. Elizabeth Gosling, Regional Technical College, and Zoology Department, University College, GALWAY, Ireland.

The controversy concerning the systematic position of *Mytilus galloprovincialis* dates back to the 1860's. While some authorities regard *M. galloprovincialis* as a good species, other consider it a variety of the larger *M. edulis* species complex. Separation of *M. edulis* and *M. galloprovincialis* has traditionally been based primarily on shell morphology. The first part of this paper evaluates the morphological criteria used to separate the two forms of mussel. It is concluded that with few exceptions, e.g. areas in S. W. England, no single morphological character can reliably be used to separate mixed populations of the two mussel types in Western Europe. This is especially true for regions such as the Atlantic coasts of Ireland, parts of Scotland and North East England where there is extensive hybridization and introgression occurring between the two forms. In recent years, other techniques, e.g. gel electrophoresis, cytology, immunology and artificial hybridization, have been applied to the problem. The second and major part of the paper reviews the results of such studies. On the basis of the evidence to date, it is concluded that the *M. galloprovincialis* form does not merit the rank of full species but appears to be a race or subspecies of *M. edulis.*

EXCESS OF ALLOZYME HOMOZYGOSITY IN MARINE MOLLUSCS AND ITS POSSIBLE BIOLOGICAL SIGNIFICANCE. S. M. Singh and **R. H. Green,** Department of Zoology, University of Western Ontario, London, Ontario, Canada.

Several studies of electrophoretically detected enzyme variations have reported homozygote frequencies higher than expected under panmixia and random mating.

Such excess of homozygosity has repeatedly been observed in species of marine molluscs, including *Crassostrea, Littorina, Macoma, Modiolus* and *Mytilus*. Possible explanations for such an observation fall in four categories: inbreeding, presence of null alleles, Wahlund effect and selection. These species are in general dioecious with external fertilization, and therefore avoid inbreeding. An excess of homozygosity has been observed for a number of enzyme loci. The presence of many common null alleles on all these randomly selected polymorphic loci is not likely. Aspects of the Wahlund effect (a consequence of sampling over populations each of which behaves as a separate Mendelian population), and of selection are presented using data on *Crassostrea, Macoma* and *Mytilus*. The data on excess of homozygosity, presented here, has three special features: (1) The degree of this excess is dependent on age and stage of development, higher in individuals of younger than of older age groups; (2) Degree of homozygosity has a negative correlation with growth rate and with metabolic efficiency; and (3) slow growers have a higher post-settlement mortality rate. Such results could not be eplained by the Wahlund effect. These observations permit us to offer an hypothesis for the origin and existence of excess homozygosity observed in these species with pelagic larvae. Depending on the species the pelagic larval period may range from three to four weeks after which they settle to form spat and grow to maturity. Furthermore, the time to first spawning tends to be a function of size rather than age, and individuals continue to reproduce after first spawning as long as they stay in the population. This model could be viewed as a form of balancing selection, where the relative fitness of homozygotes and heterozygotes is different during the pelagic larval phase from stages following settlement. Differential fitness based on development stages has been reported in other organisms.

POSSIBLE EXPLANATIONS OF HETEROZYGOTE DEFICIENCY IN MARINE MOLLUSCS. **E. Zouros** and **D. W. Foltz,** Dalhousie University, Halifax, Nova Scotia.

Many studies of natural populations of marine molluscs have shown heterozygote deficiency at enzyme loci. This phenomenon is prevalent in an oyster population that we have studied for the last five years (Singh and Zouros, 1978; Zouros et al., 1980). Elsewhere, we have presented arguments against the hypothesis of inbreeding (Zouros et al., 1980) and population mixture (Zouros et al., submitted). Here, we examine selection models that may generate heterozygote deficiency without genetic differentiation. In particular we consider the following three models. (1) Viability rates are reversed from the planktonic to the post-settlement stage. Under this model, heterozygote deficiency may appear when the population is scored after settlement but before adult selection is completed. The condition for this situation to obtain is that the gene selected against in the larval stage be dominant (in its selective effect) over the gene selected for. Therefore, underdominance is not a necessary condition for heterozygote deficiency. (2) Viability selection is confined to the larval stage and is compensated by differential fecundity in the adult stage. This model may generate post-settlement heterozygote deficiency and, again, for this event to occur there is no need for underdominance in larval viabilities. (3) This model considers genotype-dependent spawning time. When homozygotes spawn at different times than heterozygotes, there will occur in a population a heterozygote deficiency whose equilibrium value depends on the gene frequency and the coefficient of overlap between the spawning times of homozygotes and heterozygotes. Overdominance for fecundity will enhance the effect of genotype-dependent spawning. The models are based on the observation that in the American oyster, heterozygotes attain larger size, thus producing more gametes than homozygotes, and may also have lower postsettlement mortality rates. The genotypic and phenotypic data from a large one-year-old oyster cohort are used to test the plausibility of the models.

POPULATION GENETICS AND TAXONOMIC INFERENCE. **Steven M. Chambers,** Office of Endangered Species, Washington, D.C.

Methods developed by molecular geneticists to separate isoenzymes have made available for study a large number of genetic loci. The appropriate population genetic analyses of these loci and their use in making taxonomic inferences is reviewed using specific examples.

Although there is a correlation between divergence at these loci and taxonomic divergence in well-studied groups, there is a high variance associated with measures of genetic divergence that limits the utility of these data in making taxonomic inferences concerning allopatric populations. Isoenzyme data are still of some use for classification of allopatric populations below the generic level. In these cases, the application of isoenzyme data generally follows criteria similar to those used for measures of morphological divergence. Description of allopatric species or subspecies based solely on isoenzymes can rarely be justified.

Different criteria are appropriate for making taxonomic inferences from isoenzyme data for sympatric populations of possible sibling species. In these cases, population genetic analyses of deviations of genotype frequencies from Hardy-Weinberg equilibrium expectations and maximum likelihood analyses of multilocus genotypes are appropriate.

GENETIC RELATIONSHIPS AMONG NORTH AMERICAN PLEUROBEMINI AND AMBLEMINI (BIVALVIA: UNIONIDAE) WITH EMPHASIS ON *ELLIPTIO, UNIOMERUS, ELLIPTOIDEUS,* AND *QUINCUNCINA*. **George M. Davis,** Academy of Natural Sciences of Philadelphia, Pennsylvania.

Allozyme analyses over 14 loci were used to assess the molecular genetic relationships among 39 populations pertaining to 24+ species. The distribution of species per genus was: *Elliptio*(14+), *Fusconaia*(2), *Uniomerus*(3), *Elliptoideus*(1), *Quincuncina*(1), *Megalonaias*(1), *Quadrula*(1). The outgroup comparator was *Lampsilis*(1; tribe Lampsilini). A matrix of Nei's genetic distances was used in multivariate procedures to produce a two dimensional diagram of OTU projections on the first two Principle Components following 3D scaling; a Prim network was used.

The purposes of these analyses were: 1) to determine the relationships among species of *Elliptio* where several populations of lanceolate taxa with different shell phenotypes were involved; 2) to determine the relationships between *Uniomerus* and *Elliptio;* 3) to determine the relationships of *Elliptoideus* and *Quincuncina* to genera assigned to the tribes Pleurobemini and Amblemini (in: Davis and Fuller, 1980). No. 3 was done because of uncertainty of these relationships following immuno-electrophoretic studies (Davis and Fuller, 1980). Individual heterozygosity (H) and frequencies of polymorphism (P) were assessed in relationship to species and higher taxa. *Uniomerus* is divergent from *Elliptio* yet clearly in the same tribe, the Pleurobemini. The amount of genetic divergence among species of *Uniomerus* approximates the greatest divergence among species of *Elliptio. Elliptoideus* and *Quincuncina* group with other genera of the Amblemini. There appear to be three separate clades of lanceolate *Elliptio. Fusconaia succissa* and *F. flava* clearly belong in different genera.

Parameter H has high variance among species. Variance within a species is seen for *Elliptio complanata;* $\overline{X}$ = .146 ± .032 (.119 − .214; N = 8). Lanceolate taxa of *Elliptio* had $\overline{X}$ H of .096 ± .047 (.021 − .173). Topotype *E. lanceolata* had the lowest H, 0.021. Highest values of H were found in the *E. crassidens* group of related taxa: E_{cr}^{5}, .212; Ec^{28}, .214.

USE OF MOLECULAR GENETICS TO DISTINGUISH SPECIES OF THE GASTROPOD GENUS *CREPIDULA*.

K. Elaine Hoagland, Academy of Natural Sciences, Philadelphia, Pennsylvania.

Populations of *Crepidula convexa* and *C. plana* were collected in mangroves near Ft. Pierce, Florida. They were found to differ from New England populations in the mode of larval development, although this character is not known to vary intraspecifically in the genus. Allozyme studies were conducted to assess the genetic differences between the Ft. Pierce and northern populations. Horizontal starch gel electrophoresis resolved 24 loci for about 100 individuals of each population. Two populations each of the Floridian *C. convexa* and *C. plana* were compared with three each of the same species from New England. To assess the typical amount of genetic difference within and between species, seven populations of *C. fornicata* and one each of Californian *C. onyx* and Brasilian *C. protea* were electrophoresed. The populations of *C. fornicata* clustered tightly, with Nei's distance values (D) of .003-.016. The two Floridian *C. convexa* were separated by D = .008 while the average separation of three populations of northern *C. convexa*'s was .054. The two groups coalesced at .745, using a simple unweighted averaging technique. For southern and northern *C. plana,* D values were .045 and .081, respectively; the groups coalesced at .393. *C. convexa* greater difference between regions is due to fixation of alternate alleles at 46% of the loci. *C. plana* is characterized more by large differences in allele frequencies; only 21% of the loci are fixed for alternate alleles. In both cases, many alleles are unique to one geographical region. These data demonstrate reproductive isolation between the Ft. Pierce and northern populations of both species, especially *C. convexa.* Because the populations are allopatric, electrophoretic data alone cannot conclusively delineate species. D values over .30 are strong indicators of speciation, based on data from other taxa, but in this study, divergence between known species of *Crepidula* (e.g. *C. fornicata* and *C. plana*) was greater than that between either of the potential sibling species pairs being tested. Calculations based on Robers' distance gave similar results.

GENETIC POPULATION STRUCTURE AND BREEDING SYSTEMS IN TERRESTRIAL SLUGS OF THE FAMILIES ARIONIDAE, LIMACIDAE (MOLLUSCA: PULMONATA).

David W. Foltz, and **Robert K. Selander,** University of Rochester, Rochester, New York.

Genetic variation detected by electrophoresis of enzymes was surveyed in populations of nine arionid species and seven limacid species of terrestrial slugs in Great Britain, Ireland, and France. In each family, average individual heterozygosity ($\bar{H}_o$) varied widely across species, from zero in some (*Arion circumscriptus, A. silvaticus, A. intermedius*) to 0.19 (*A. distinctus* and *Deroceras reticulatum*). Whereas no limacid slug studied to date has been found to lack genetic heterozygosity, our research indicates that four arionid species consist of monogenic (homozygous) strains: *A. intermedius, A. circumscriptus, A. fasciatus,* and *A. silvaticus.* This result suggests that self-fertilization is a less frequent breeding system in the Limacidae than in the Arionidae. The amount of heterogeneity in allele frequency among geographic samples of a species was not correlated with heterozygosity, but it was associated with breeding system: facultatively-selfing slugs (*A. ater, A. subfuscus,* and *D. laeve*) exhibit higher levels of allele frequency heterogeneity than do outcrossing species. In both the Limacidae and the Arionidae, the highly heterozygous species are major agricultural pests, whereas those with lower levels of heterozygosity occur in agricultural habitats less frequently or not at all.

ANNUAL BUSINESS MEETING
REPORT FOR 1982

The annual business meeting of the American Malacological Union was called to order by President Louise Russert-Kraemer at 2:10 p.m. in the Carnival Room of Fountain Bay Club Hotel in New Orleans, Louisiana, Friday 23 July 1982.

Minutes of the 1981 meeting as printed in the 1981 *Bulletin* were approved with restatement of a motion due to the omission of a line: "The chairman of the common names committee is empowered to explore sources of grant funding from appropriate agencies to aid in completion of their work. Any grant proposed must be approved by the president and treasurer of the AMU prior to submittal to the agency or agencies involved."

Reports from officers and committees were summarized and have been filed with the Recording Secretary. Membership and subscriptions for fiscal year 1981 totalled 774, a gain of 26.

Dr. Alan Kohn discussed plans for the approved meeting, August 7–13, 1983, at Seattle, Washington, with housing on the campus of the University of Washington. Symposia include "Molluscan Nerve Cells" and "Molluscan Extinctions." Midweek field trips and an optional field trip to Friday Harbor after the meeting are planned. Workshops on Cephalopods, Pacific Northwest Marine Mollusks and malacological publications are scheduled.

A motion was approved as follows: "The request from President David Lindberg to have the Western Society of Malacologists join AMU in the Seattle meeting in 1983 is approved. Proceeds from WSM's shell auction held to provide awards to students will be split with AMU in 1983, and WSM will print it's own meeting report. Other details on abstracts in the *Bulletin* and other items such as availiability of the *Bulletin* to WSM participants will be worked out between the presidents."

Motion approved to accept Dr. Robert Robertson's plans to hold the 1984 meeting July 22–27 at the Holiday Inn Scope Convention Center at Norfolk, Virginia. Plans include an international symposium on the physiological ecology of nonmarine molluscs to be organized by Dr. W. D. Russell-Hunter, Dr. Albert J. Burky, and Dr. Robert F. McMahan. An auction of books, reprints, and shells is planned. Field trips will be midweek.

The budget voted for 1983 included a raise in dues as follows:

New member or reinstatement fee remains the same at	$ 1.50	
Regular Member (Anywhere in Western Hemisphere) (Air delivery available outside U.S. + postage charge)	15.00	
Additional Family Member, each (remains the same)	1.00	
Sustaining Member, $25.00 donation plus dues, annually	40.00	
Corresponding Member (anywhere outside Western Hemisphere)	15.00	+ postage
Affiliate Membership for shell clubs and other similar organizations	17.00	
Affiliates as above, outside Western Hemisphere	17.00	+ postage
Subscription rate (includes sea mail; airmail available with postage)	18.00	

Budget for 1983:

INCOME

Memberships (All types except life members)		$10,271.00
Sales		
HTSCS		300.00
Rare & Endangered booklet reprint		20.00
Bulletin, back issues		200.00
Teskey Index		50.00
	SUBTOTAL SALES:	(570.00)
Page charges to authors		2,084.00
Proceeds of meeting		1,000.00
Donations, Symposium		1,000.00
Miscellaneous		113.00
	TOTAL:	$15,038.00
Interest, Savings (Not added to income)		(450.00)

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DISBURSEMENTS

Bulletin		$ 7,500.00
Newsletters		1,000.00
Conservation Committee		50.00
Membership Committee		25.00
President's Organizing Fund		600.00
California Filing Fee		7.50
Officers to Meetings (Secretaries, Treasurer, Editor)		2,200.00
Legal Defense		50.00
Postage (except Bulletin and Newsletters)		900.00
Printing (except Bulletin and Newsletters)		500.00
Office Supplies		97.50
Postal Permit		45.00
Miscellaneous		200.00
Annual Meeting Expense		150.00
Ads of Meeting & HTSCS, etc.		548.00
Memberships WSM, ASC, etc.		45.00
Symposia Expenses		870.00
Student Prize (paper)		250.00
	TOTAL:	$15,038.00

A motion concerning a new endowment fund was approved as follows:

> "Unexpended monies which have been received in past years which were intended for the Symposium Fund are to be segregated from the general fund and placed into a separate interest bearing account to be known as the AMU Symposium Endowment Fund; and further that all future donations to the Symposium Fund be placed in this same account with the exception of certain additional funds which may be earmarked by the donor for use in a certain year; and further that the President of the AMU may use only the interest from this Endowment Fund for Symposium expenses; and further that the AMU Council make a formal effort, on an annual basis, to increase the principal of the fund."

Officers elected include:

President:	Alan J. Kohn, one year term
President-elect:	Robert Robertson, one year term
Vice-President:	Melbourne Carriker, one year term
Recording Secretary:	Constance E. Boone, three year term
Councillors-at-large:	Virginia Vail and Carl Gugler, two years terms

Other officers for 1983 include: (in terms)

Treasurer:	Myra L. Taylor
Corresponding Secretary:	Paul R. Jennewein
Councillors-at-large:	James Nybakken and Dick Petit
Editor:	Robert Prezant (appointed 1982)

Other motions brought from Council were approved as follows:

1. "An article explaining the role of the Council of Systematic Malacologists will be written by Dr. Fred Thompson for the AMU Newsletter."
2. "Dave Stansbery should delegate the responsibility to individual scientists to obtain common names for molluscan species in North America north of Mexico and to the 200 meter depth. The lists will be reviewed by the standing committee with a final list presented to Council by next year's annual meeting."
3. Motion on AMU publication includes:
   "1) The AMU *Bulletin* will be printed by Braun-Brumfield of Ann Arbor, Michigan;
   2) Standards for paper stock, column format, print size, table composition will be set;
   3) Printing costs will be offset by page cost charges to those with grant and institutional support and with 30% profit on reprints;
   4) Starting with the 1982 issue the *Bulletin* will be given a volume number;

   5) All manuscripts submitted will be sent out for peer review;
   6) All authors will receive page proofs for corrections;
   7) The editorial, printer, manuscript qualities and journal quality will be subject to review and advice of a three-member board of professionally qualified editors."

4. "The next AMU *Bulletin* will have an errata sheet included that corrects errors on page 26 of the 1981 *Bulletin,* that lists the contributors of the symposium (page 26) in a revised Index and that all abstracts for the symposium papers be published as errata."
5. "Page charges shall be mandatory for articles over 300 words in length, such charges shall cover estimated costs of typesetting and printing. Waiver of such charges may be made by the publications committee if funds are not available from the author or their institutions."
6. A memorial fund motion approved as follows: 'The Joseph C. Bequaert Award for Field Studies of Land or Freshwater Mollusks will be made with a grant of $400.00 to be awarded to a graduate student for the purpose of conducting field studies of land or freshwater mollusks. Grant proposals should include: (1) A brief description of the proposed project, (2) an estimated budget of anticipated expenditures, and (3) a statement from the student's supervising professor that the project is an appropriate part of the student's research. Proposals must be submitted in quadruplicate by January 1, 1983, to the President of the American Malacological Union for forwarding to the Review Committee, and the announcement of the award will be made by April 1, 1983. The above statement shall be approved for publication in the appropriate journals and the President of the AMU shall be authorized to appoint a three-member Review Committee whose qualifications should include membership in the AMU and having supervised research involving field studies in malacology. An appropriate expression of thanks shall be extended to Dr. Bequaert's son and daughter, and they shall be informed concerning the award and how it is used."
7. "The incoming president is directed to appoint a constitution committee to examine and possibly modify the Constitution and By-Laws in the areas of endowment funds, special gifts, editorial board (Publications Committee) and other areas that may be identified. Recommended changes should be handled in such a way as to be approved at the 1983 AMU meeting."
8. "The appropriate mechanism for resolution of nomenclatural problems rests in a small working group rather than a formal symposium."
9. "The next dues notices of the AMU will be altered to include the following information after the basic listing of dues:

"The AMU is attempting to build a Symposium Endowment Fund and to increase student participation. We thus solicit your tax deductible gifts for the following purposes:

(1) Add to Symposium Endowment Fund ______
(2) Prize for best student paper presented at the next AMU meeting ($250.00 goal) ___
(3) Help publish papers of students in the forthcoming *Bulletin* ($1,000 goal) ______
Total added gifts ______
Total amount paid ______"

10. "The President is requested to obtain the negative of this year's annual meeting so that larger photographs could be printed and sent to those requesting them."

Dr. Kraemer expressed great appreciation for the years of service to AMU given by Dr. Dee Dundee in her capacity as Editor of the *Bulletin*. She announced Dr. Dundee's resignation. She presented Dr. Robert Prezant as Editor of the AMU *Bulletin.*

Motion approved giving a vote of commendation and thanks to President Louise Kraemer. Adjournment came at 3:30 p.m.

Constance E. Boone, Recording Secretary

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1981

CHECK BOOK BALANCE, JANUARY 1, 1981			$ 6,252.57
RECEIPTS:			
Memberships:			
Regular	$ 5,094.00		
Sustaining	253.00		
Corresponding	293.00		
Clubs & institutions, domestic	804.00		
Clubs & institutions, foreign	199.00		
Subscriptions	99.00		
	6,742.50	6,742.50	
Sales:			
HOW TO STUDY & COLLECT SHELLS	337.25		
RARE & ENDANGERED SPECIES	32.50		
TESKEY INDEX	20.00		
AMU BULLETIN, Back issues	183.00		
	572.75	572.75	
Other Receipts:			
Page charges to authors	612.50		
Symposium donations	960.52		
Miscellaneous receipts	83.80		
Fort Lauderdale meeting proceeds (Includes auctions, etc.)	5,095.22		
	6,752.04	6,752.04	
TRANSFERRED FROM SAVINGS ACCOUNT:	3,000.00	3,000.00	
TOTAL CASH ACCOUNTED FOR:		17,067.29	17,067.29
TOTAL CASH HANDLED:			$23,319.86
DISBURSEMENTS:			
AMU BULLETIN, incl. postage, printing, etc.	$ 6,241.93		
AMU NEWSLETTER, incl. postage, printing, etc.	863.31		
President Houbrick's expenses	526.00		
President Elect Kraemer's expenses	320.00		
Other postage	580.27		
Other printing	362.91		
Office supplies	92.96		
California filing fees	7.50		
Dues to other organizations	65.00		
Symposium expenses	2,392.48		
Ads for meetings	832.00		
Student award	250.00		
Typewriter repair	47.50		
Expenses of officers to meeting	1,688.32		
Expenses for Fort Lauderdale meeting	286.49		

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Petty cash account for editor	150.00		
Bank charges, returned checks, refunds, etc.	49.55		
Miscellaneous expenses	302.10		
Total disbursements from all activities	$15,058.32	15,058.32	
CHECK BOOK BALANCE, JANUARY 1, 1981			$ 6,252.57
TOTAL RECEIPTS			17,067.29
TOTAL CASH			$23,319.86
TOTAL DISBURSEMENTS			15,058.32
CHECK BOOK BALANCE, DECEMBER 31, 1981			8,261.54

SASA* savings account #5-034514	$ 7,988.03
Interest for 1981	354.92
Transfer to checking account	3,000.00
Transfer to certificate of deposit #22-906859	2,000.00
Total for account	3,342.95
SASA* certificate of deposit #22-906859	2,000.00
Interest for 1981	98.91
Total for account	2,098.91
SASA* certificate of deposit #5-904812 AMU Life Membership Fund	2,954.76
Interest for 1981	139.34
Total for account	3,094.10
Transferred entire account #5-904812 to certificate of deposit #22-906860 for higher interest rate, September 16, 1981, SASA*	3,094.10
Interest for 1981	153.02
Total for account (Life Membership)	3,247.12

*SASA = San Antonio Savings Association

RECAPITULATION OF ASSETS, DECEMBER 31, 1981:

Cash in checking account, Mercantile Bank		$ 8,261.54	
Treasurer's petty cash fund		20.00	
Secretary's petty cash fund		175.00	
Editor's petty cash fund		150.00	
SASA* Account #5034515		3,342.95	
SASA* Account #22-906859		2,098.91	
TOTAL ASSETS		$14,048.40	
LIFE MEMBERSHIP ACCOUNT #5-904812	-0-		
LIFE MEMBERSHIP ACCOUNT #22-906860	$ 3,247.12		
AMU NET WORTH, DECEMBER 31, 1981			$14,048.40
CHANGES IN CAPITAL ACCOUNT:			
AMU Capital Account, January 1, 1981			$14,435.60
AMU Capital Account, December 31, 1981			14,048.40
NET DECREASE IN ASSETS			$ 387.20

Respectfully Submitted,
Myra L. Taylor, Treasurer

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1982–1983

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(Revised November 26, 1982)

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ALLEN, DR. J. FRANCES, Rt. Box 1039, Front Royal, VA 22630.
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ANDERS, KIRK W., Shells of the Seas, Inc., P.O. Box 1418, Ft. Lauderdale, FL 33302 (Volutidae; all rare shells).
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ATHEARN, HERBERT D., Museum of Fluviatile Mollusks, Rt. 5, Box 499, Cleveland, TN 37311 (Freshwater mollusks).
ATHEARN, MRS. ROY C. (ELEANOR), 5105 N. Main St., Fall River, MA 02720 (Land shells).
AUFFENBERG, KURT, Museum Technician, Florida State University, Univ. of Florida, Museum Road, Gainesville, FL 32611 (Neritacea: Neritidae).
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AVERY, MRS. R. GAIL, Box 2557, Harbor, OR 97415 (West American shells; exchange).
AVILES, E., PROF. MIGUEL C., Apartado 6-765, Zona Postal El Dorado, Panama, Rep. of Panama (Histology and embryology).
BABRAKZAI, DR. NOORULLAH, Dept. of Biology, Central Missouri State University, Warrenburg, MO 64093.
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BARGAR, TOM and DENISE SCHNEIDER-BARGAR, 1235 N. 7th St., Lincoln, NB 68508 (Functional morphology of gastropods).
BARLOW, MRS. G. BARTON (ALICE), 76 Westervelt Ave., Tenafly, NJ 07670.
BATTEN, DR. ROGER L., American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024 (Fossil and recent Pleurotomarians).
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BAZATA, KENNETH R., Ecological Analysts, 221 Oakcreek Drive, Lincoln, NE 68528 (Terrestrial pulmonates; *Dentalium*).
BEETLE, MS. DOROTHY E., director, Patterson Planetarium, 2900 Woodruff Farm Road, Columbus, GA 31907 (U.S. land and freshwater mollusks).
BERCOVITZ, DR. ARDEN BRYAN, c/o Research Dept., San Diego Zoo, P.O. Box 551, San Diego, CA 92112 (Reproductive biology and gonadal function).
BERGMANN, JOSEPH A., Rt. 3, Box 3064, Boerne, TX 78006 (Land and freshwater mollusks, recent and fossil).
BERMUDEZ, ALEJANDRO, P.O. Box 68, Missouri City, TX 77459 (*Murex* and nudibranchs from the Caribbean zone).
BERRY, DR. ELMER G., 8506 Beech Tree Court, Bethesda, MD 20034.
BERRY, DR. S. STILLMANN, 1145 W. Highland Ave., Redlands, CA 92373.
BIANCHI, MR. and MRS. ROBERT, Box 235, Goodland, FL 33933.
BICKEL, DAVID, 613 West Ave. C, Bismarck, ND 58501 (Systematics and ecology of freshwater mollusks, esp. pleurocerid snails).
BIJUR, JEROME M., 135 Seventh Ave. N., Naples, FL 33940 (Buy, exchange Florida and Caribbean marine and Gulf of Mexico mollusks).
BIPPUS, MRS. ALVIN, 2743 Sagamore Rd., Toledo, OH 43606 (Marine gastropods).
BISHOF, DAVID, 994 68th St. Ocean, Cayo Vaca, FL 33050.
BLAIR, LUCIANNE, 1033 Rockcreek Drive, Port Charlotte, FL 33952.
BLAISTEN, DR. LIA O.B. DE, Nicolas San Juan 1535, Colonia del Valle, Mexico D.F., Mexico 03100 (Scientist amateur—American and Caribbean seashells; cowries and *Strombus*).
BLEAKNEY, DR. J. SHERMAN, Dept. of Biology, Acadia University, Wolfville, Nova Scotia, Canada BOP 1XO (Nudibranchs, sacoglossans; ecology, zoogeography, systematics).

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BLEDSOE, WILLIAM D., 352 Bon Hill Rd., Los Angeles, CA 90049.
BODY, RALPH L., 2438 10th Ave. W., Seattle, WA 98119 (Taxonomy).
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BOND, MIRIAM, 111 Sheldon, Ames, IA 50010 (Limpets).
BORROR, KATHY GAIL, Museum of Zoology, OSU, 1813 N. High St., Columbus, OH 43210.
BOSS, DR. KENNETH JAY, MCZ, Harvard University, Cambridge, MA 02138.
BOWERS, RAYMOND E., 128 E. Oakland Ave., Columbus, OH 43201 (Freshwater ecology of naiades).
BOYD, DR. and MRS. EUGENE S., R #1, Box 549, Bokeelia, FL 33922 (All shells).
BRAND, DR. TIMOTHY, 4120 38th St., #17, San Diego, CA 92015 (Eulimid gastropods parasitic on/in marine organisms).
BRANDAUER, MRS. NANCY E., 1760 Sunset Blvd., Boulder, CO 80302.
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BRENCHLEY, DR. GAYLE A., Assist. Prof., Dept. of Ecology and Evolutionary Biology, Univ. of Calif., Irvine, CA 92717 (Distribution, migration and experimental life history of mudsnails, *Ilyanassa obsoleta*).
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BUCHANAN, ALAN C., Missouri Dept. of Conservation, Fish and Wildlife Research Ctr., 1110 College Ave., Columbia, MO 65201 (Fisheries biologist).
BUCHER, ANITA P., 7504 Branchwood Drive, Mobile, AL 36609 (Taxonomy).
BUCKLEY, GEORGE D., 164 Renfrew St., Arlington, MA 02174.
BURCH, DR. JOHN B., Museum of Zoology, Univ. of Mich., P.O. Box 2749, Ann Arbor, MI 48106 (Land and freshwater mollusks).
BURCH, MRS. JOHN Q., 1300 Mayfield Rd., Apt. 61-L, Seal Beach, CA 90740.
BURCH, DR. TOM and MRS. BEATRICE L., P.O. Box 309, Kailua, HI 96734 (BLB, planktonic mollusks; TAB, deep water mollusks).
BURGER, SYBIL B., 3700 General Patch N.E., Albuquerque, NM 87111 (Gulf of Mexico mollusks; land snails).
BURKE, MRS. ALLAN L., 18128 Lakeside Lane, Nassau Bay, TX 77058.
BURKY, DR. ALBERT J., Dept. of Biology, Univ. of Dayton, Dayton, OH 45469.
BUROKER, DR. NORMAN E., Bur. of Biological Research, P.O. Box 1059, Rutgers State University of New Jersey, Piscataway, NJ 08854 (Evolutionary and population genetics of pelecypods).
BUTLER, NANCY M., Dept. of EPO Biology, University of Colorado, Boulder, CO 80309.
CAKE, DR. EDWIN W., JR., Head, Oyster Biology Section, Gulf Coast Research Laboratory, East Beach, Ocean Springs, MS 39564 (Oysters, cestode parasites of marine mollusks, mariculture of estuarine mollusks).
CALDWELL, DR. RONALD S., Dept. of Biology, Texas College, Tyler, TX 75701 (Terrestrial gastropods of Kentucky).
CALL, SAM M., 107 Goodrich Ave., Lexington, KY 40503 (Pelecypods).
CALNAN, THOMAS R., Univ. of Texas Bureau of Economic Geology, University Station Box X, Austin, TX 78712 (Gulf Coast mollusks).
CAMPBELL, MINNIE LEE and DONALD C., 3895 DuPont Circle, Jacksonville, FL 32205 (General).
CAPO, THOMAS R., 59 Nickerson St., E. Falmouth, MA 02536 (Benthic ecology).
CARLTON, DR. JAMES T., Mystic Seaport Museum, Mystic, CT 06355 (Estuarine and brackish water mollusks).
CARNEY, CDR. W. PATRICK, MSU USN, 12900 Turnbrook Parkway, Rockville, MD 20851.
CARRIKER, PROF. MELBOURNE R., College of Marine Studies, Univ. of Delaware, Lewes, DE 19958.
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CASTAGNA, MICHAEL, Virginia Institute of Marine Science, Wachapreague, VA 23480 (Pelecypod larval behavior).
CASTIGLIONE, MARIE C., 5832 S. Alameda Apt. C, Corpus Christi, TX 78412 (Gulf of Mexico mollusks).
CATE, MRS. CRAWFORD N. (JEAN M.), P.O. Drawer 710, Rancho Santa Fe, CA 92067 (*Mitra, Cypraea*; no exchanges).
CHADWICK, ALBERT F., 2607 Turner Rd., Wilmington, DE 19803 (Marine shells).
CHAMBERS, DR. STEVEN M., OES, U.S. Fish & Wildlife Service, Dept. of the Interior, Washington, D.C. 20240.
CHANLEY, PAUL and MATTIE, P. O. Box 12, Grant, Fl 32949.
CHICHESTER, LYLE F., Dept. Biological Sciences, Central Conn. State College, 31 Chamberlain St., New Britain, CT 06052 (Ecology of terrestrial gastropods, biology of land slugs).
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CHRISTIE, DR. JOHN D., Dept. of Pathology, Univ. of Texas Medical Branch, Galveston, TX 77550.
CHROSCIECHOWSKI, PRZEMYSLAW K., APTDO 125, Maracay, Venezuela 2101A (Planorbidae).
CHUNG, DANIEL, Museum of Zoology, Univ. of Michigan, Ann Arbor, MI 48104 (Pulmonates; Hawaiian mollusks).
CLARK, DR. KERRY B., Dept. of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901 (Opisthobranchs).
CLARKE, DR. ARTHUR H., Ecosearch, Inc., 7 Hawthorn St., Mattapoisett, MA 92739.
CLENCH, DR. WILLIAM J., 26 Rowena St., Dorchester, MA 02124 (Land shells in all of the West Indies—freshwater mollusks in North America).
CLOVER, PHILLIP W., P.O. Box 83, Glen Ellen, CA 95442 (Rare *Cypraea, Conus, Voluta, Murex* and *Marginella*—buy and exchange).
CLYMER, GEORGE M., Minnesota Dept. of Natural Resources, Ecological Services Section, Box 25, 658 Cedar St., St. Paul, MN 55155 (Unionids).
COAN, DR. EUGENE V., 891 San Jude Ave., Palo Alto, CA 94306.
COLE, DR. TIMOTHY JAMES, Horn Point Environmental Laboratory, University of Maryland, Box 775, Cambridge, MD 21613 (Genetic divergence among molluscan populations; ecological-genetic interdigitations).

COLEMAN, DR. RICHARD W., Dept. of Biology, Upper Iowa University, Fayette, IA 52142 (Environmental interrelationships, plants-invertebrates).
COLMENARES, PAUL PERAZA, Lra Transversal de Sebucan, Quinta "Don Raul", Caracas, Venezuela 107 (Taxonomy and effects of pollutants on mollusks).
COMPITELLO, MRS. JULIETTE, 5630 Alta Vista Road, Bethesda, MD 20034.
CONEY, C. CLIFF, Dept. of Biology, Coastal Carolina College, Univ. of South Carolina, Conway, SC 29526 (Evolutionary biology of terrestrial and freshwater molluscs).
CONKLIN, WILLIAM A., R.T. (FASRT), President, Inner Dimension, 1571 Marshall Ave., Orangeburg, SC 29115 (Radiography/photography).
COOK, BUNNIE and GEORGE, 1120 Makaiwa St., Honolulu, HI 96816 (Marine—Mitridae and other families).
COOK, DR. SUSAN B., The Bunting Institute of Radcliffe College, 10 Garden St., Cambridge, MA 02138 (Behavioral ecology of tropical marine gastropods; behavioral ecology of freshwater gastropods).
COOPER, ROBERT W., 5012 Pfeiffer Road, Peoria, IL 61607 (Florida marine; world *Murex, Pecten, Spondylus;* Scuba).
COOVERT, GARY A., 36 Prospect Ave., Dayton, OH 45415 (Taxonomy of worldwide Mollusca; esp. Pectinidae).
CORGAN, DR. JAMES X., Dept. of Geology, Austin Peay State Univ., Clarksville, TN 37040 (Pyramidellidae, Vitrinellidae, scaphopods, Tertiary faunas).
CORPENING, JOHN T., 324 NE 81st St., Seattle, WA 98115 (Marine coral dwelling gastropods).
CORPUZ, GLADYS, C., Dept. of Zoology, University of Hawaii, Honolulu, HI 96822 (Life history and ecology).
COSMAN, DIETER, 7 Oak Hill Rd., Huntington, NY 11743 (Marine tropical and subtropical Gastropoda and Bivalvia worldwide).
COVEY, JEWELL M., 5666 E. Hampton, Apt. 270, Tucson, AZ 85712 (Panamic Province and Epitoniacea worldwide, Calif. and Northwest mollusks).
CRAMER, FRANCES L., 766 Obispo Ave., Long Beach, CA 90804 (Ecology; conservation).
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CUMMINGS, RAYMOND W., 37 Lynacres Blvd., Fayetteville, NY 13066 (West Indian shells, esp. Windward and Grenadine Islands).
CUMMINS, HAYS, Dept. of Oceanography, Biology Section, Texas A&M University, College Station, TX 77843 (Benthic ecology).
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D'ASARO, CHARLES N., University of West Florida, Pensacola, FL 32503 (Reproduction and development of prosobranchs).
DAVENPORT, MRS. LILLIAN B., 802 Cape Ave., Box 81, Cape May Point, NJ 08212 (All marine mollusks).
DAVIS, DR. DEREK S., Nova Scotia Museum, 1747 Summer St., Halifax, NS B3M 3A6, Canada (Gastropod biology and taxonomy).
DAVIS, DR. GEORGE M., Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, PA 19103.
DAVIS, DR. JOHN D., 25 Old Homestead Rd., P.O. Box 156, Westford, MA 01886 (Ecology of marine bivalves).
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DEYNZER, ALBERT E. and BEVERLY A., Showcase Shells, 1614 Periwinkle Way, Sanibel, FL 33957 (Marine mollusks).
DEYRUP-OLSEN, DR. INGRITH, Dept. of Zoology, NJ-15, University of Washington, Seattle, WA 98195 (Physiology of fluid exchange; mucus formation).
DIETRICH, MR. and MRS. LOUIS E. (GERTRUDE B.), 308 Veri Drive, Pittsburgh, PA 15220.
DILLEY, DONALD R., Div. of Plant Industry, principal staff entomomologist; Dept. of Food and Agriculture, State of Calif., Room 304, 1220 N. St., Sacramento, CA 95814 (Mollusks of economic importance to agriculture).
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DIMATTEO, TONY, #U-5824, Tallahassee, FL 32313 (Opisthobranch and gastropod defensive mechanisms, predator-prey interactions).
DOYLE, PATRICIA, 336 Pine Ave., St. Lambert, Quebec, Canada J4P 2N8.
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EDWARDS, D. CRAIG, Dept. Zoology, Morrill Science Center, University of Massachusets, Amherst, MA 01003 (Population ecology and behavior of marine benthic mollusks).
EMBERTON, KENNETH C., ELLEN and LUCIA, 6044 S. Ingleside I-N, Chicago, IL 60637 (Land snails).
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ERICKSON, RICHARD J., P.O. Box 52920, Tulsa, OK 74152-0920 (Tertiary Mollusca, recent Gulf of Mexico).
EUBANKS, DR. ELIZABETH R., 57 Lyall St., West Roxbury, MA 02132 (Florida marine shells).
EVANS, SUSAN E., 244 Congress Ave., Lansdowne, PA 19050 (*Conus, Cypraea, Murex*).
EVERSOLE, DR. ARNOLD G., Ass't. Prof., Dept. of Entomology, Clemson University, Clemson, SC 29631 (Interpopulation variation and bioenergetics of molluscan populations).
EVERSON, GENE D., 5224 Northwest 17th Court, Lauderhill, FL 33313 (Worldwide collection with emphasis on Florida, Caribbean and miniatures).
EXLINE, JERRY K., P.O. Box 1267, Salina, KS (*Cypraea*).
FAIRBANKS, DR. H. LEE, Penn State University, Beaver Campus, Brodhead Road, Monaca, PA 15061 (Systematics of land gastropods; genetic variability of land gastropods).
FALLO, GLEN JAY, 1706 Hill Rise Drive, Apt. 8, Lexington, KY 4504 (Freshwater mussels, Ohioan fauna).
FEBER, OLIVE M., 4777 Sandia, Los Alamos, NM 87544 (Cones and cowries).
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FEINBERG, HAROLD S., Dept. Fossil and Living Invertebrates, American Museum of Natural History, Central Park W. at 79th St., New York, NY 10024 (Polygyridae and other U.S. Pulmonata).
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FONTANIER, DR. CHARLES E., P.O. Box 38368, Houston, TX 77238 (Unionidae; *Corbicula;* Scuba; ecology).
FOOTE, MARY K., 16204 Diana Lane, Apt. 322A, Houston, TX 77062 (Land snails and self-collected miniatures of the Texas coast).
FORRER, MR. and MRS. RICHARD B., 7660 South Boyden Rd., Sagamore Hills, OH 44067 (Accumulator of conchology and malacology literature).
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FREY, BARBARA, 1407 Park Ave., Baltimore, MD 21717 (Natural science illustrator).
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FURBISH, DEAN R., 1903 Wings Nolk, Paris, KY 40361 (Behavior, physiology of mollusks).
FUKUYAMA, ALLAN, Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039 (Taxonomy, ecology and bivalves).
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GARCIA, Dr. EMILIO FABIAN, 115 Oak Crest Drive, Lafayette, LA 70503 (Gulf of Mexico and Caribbean molluscs).
GARDNER, MRS. SANDRA M., 1755 University Ave., Palo Alto, CA 94301 (Vermetidae).
GARTON, DAVID W., Dept. of Zoology and Physiology, Lousiana State University, Baton Rouge, LA 70803 (Gulf Coast gastropods, physiology and ecology; population genetics).
GATELL, MANUEL E. and MILAGROS SANCHEZ, 13 San Jose St., Villa Clementina, Guaynabo, Puerto Rico 00657 (Caribbean seashells).
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GERBERICH, ANDREW G., 4427 S. 31st St., Apt. 102, Arlington, VA 22206 (Freshwater mussels).
GERHOLD, ROBERT M., Senior Microbiologist, Nalco Chemical Company, 1801 Diehl Rd., Naperville, IL 60540 (Environmental physiology and mollusk pest control).
GERMER, JOHN and DOROTHY, 653 Briarcliff Ave., Maywood, NJ 07607 (John—photography of shells; Dorothy—Pectens and *Murex*; shells of Eastern and Western Atlantic).
GERMON, MRS. RAYE N., 27 Rosemont Drive, Gaitherburg, MD 20760 (Muricidae, Volutidae, Mesozoic and Paleozoic fossils (marine)).
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OESCH, D. RONALD, 9 Hill Drive, Glendale, MO 63122 (Missouri mussel zoogeography).

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PEARCE, DR. JOHN B., NOAA, NMFS, Northeast Fisheries Center, Sandy Hook Laboratory, Highlands, NJ 07732 (Symbiotic relationships of crustacean (pinnotherid crabs) with mollusks: the role of mollusks in benthic communities).

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PENA MONARDEZ, RENAN D., Av. Argentina 252, Dpto. 11, Antofagasta, Chile (Taxonomy, morphology and land snails).

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QUINTANA, MANUEL G., Div. Invertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Inst. Nacional de Investigacion de las Ciencias Naturales, Av. Angel Gallardo 470, 1405 Buenos Aires, C.C. 10 suc. 5, Argentina (Non-marine Mollusca from South America) (actualmente: Paraguay y zonas limitrofes).

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SAUNDERS, DR. W. BRUCE, Dept. of Geology, Bryn Mawr College, Bryn Mawr, PA 19010 (Cephalopoda, esp. *Ectocohlia,* inc. *Nautilus*).
SCARABINO, SR. VICTOR, Instituto de Investigaciones Biologicas, Avda Italia 3318, Montevideo, Uruguay.
SCHELL, FREDERIC B., JR., 1200 Peppertree Lane, Apt. 102, Sarasota, FL 33581 Nov. 1 to June 1; The Brooklands, Colebrook, CT 06021 June 1 to Nov. 1 (Fossil shells).
SCHILLING, MR. and MRS. ALBERT E., 419 Linden Ave., Glenside, PA 19038 (Mr.—*Cypraea;* Mrs.—*Murex*; both—*Conus*).
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Cover. *Buchanania onchidioides.* Copy of original illustration of Lesson (1830), ventral view; note large cephalic tentacles and gill tips projecting over snout. See paper in this volume on *Fissurellidea* by J. H. McLean, pages 21–34.

THE AMERICAN MALACOLOGICAL BULLETIN (formerly the Bulletin of the American Malacological Union) is the official journal publication of the American Malacological Union.

AMER. MALAC. BULL. 2
February 1984

EDITORIAL COMMENT

With this issuance of volume 2 of the *American Malacological Bulletin* we end one very short lived phase of the revamped *Bulletin*'s history and initiate a new one. This will be the last issue that stands alone as a single volume. Starting with volume 3 we will produce two numbers per volume. We are able to take this important step because, as predicted, the appearance of the new *Bulletin* filled a platform for malacological publications. Following the appearance of volume 1, we saw a notable increase in manuscripts submitted to our journal. These, of course, included papers presented at our annual meeting, but also a number of "outside" papers. In this second volume almost half the papers are manuscripts submitted without prior presentation at A.M.U. meetings. Volume 3, number 1, will contain a majority of non-A.M.U. presented papers but papers of interest to all members of A.M.U. Volume 2, number 2, will report the 1984 A.M.U. meeting and contain both papers presented at the meeting as well as "outside" papers. Sustained quality of published papers will be insured by continued critical review processes.

Within the present volume we start a new column that will allow malacologists space for a give and take of ideas, opinions, and thoughts. The column, "*sententīa*" (Lat. "a way of thinking") will allow for publication of a variety of sentiments relating to malacological research and teaching. *Sententīa* begins with a report from the Council of Systematic Malacologists that outlines their views on required courses essential for training new malacologists. The column is open for discussion on this and all future reports or comments. All input will be reviewed for factual content. We hope *sententīa* opens a forum for malacologists to quickly report their thoughts on current controversies or opinions of immediate importance.

The progress of our journal reflects the important contributions all A.M.U. members have made towards our society's growth. I take this opportunity to invite continued contributions from all individuals interested in molluscs and to ask our readership for continued input and support for the progressive improvement of our publication.

The Editor

REVISION OF HIGHER TAXA IN GENUS *CERITHIDEA* (MESOGASTROPODA: POTAMIDIDAE) BASED ON COMPARATIVE MORPHOLOGY AND BIOLOGICAL DATA

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ABSTRACT

A cladistic analysis of *Cerithidea* subgenera based on morphological studies of *Cerithidea* species is presented. The morphology of *Cerithidea (Cerithideopsis) scalariformis* Say, 1825 is described and compared with observations and published accounts of other species in the genus. An account of the reproduction, spawn, development and growth of this species along with ecological observations are presented and compared with other *Cerithidea* taxa in order to summarize what is known of the biology of the genus, to develop a holistic, less arbitrary classification, and to formulate systematic definitions of the subgenera comprising it. A detailed description of the siphonal eye is given and a survey made of similar structures in other cerithiacean groups. The genus *Cerithidea*, sensu lato, is an estuarine group characterized by turreted shells with dominant axial sculpture, wide apertures, thick outer lips, and short anterior canals. The taenioglossate radula is short and all teeth bear cusps. The operculum is thin, corneous, multispiral and has a central nucleus. The ctenidium is either reduced or of broad low filaments. A simple ridge-like osphradium is present. The alimentary tract includes a pair of anterior salivary glands, a mid-esophageal crop, and a long style sac. Females have an ovipositor, a spermatophore bursa in the outer lamina and a seminal receptacle in the inner lamina of the proximal pallial oviduct. Males are aphallate. Both direct and indirect modes of development occur and growth of juveniles is rapid. Three Recent subgenera are recognized: *Cerithidea* s.s., *Cerithideopsis* and *Cerithideopsilla*, the latter subgenus being considered the most generalized (primitive).

Mesogastropods of the family Potamididae H. and A. Adams, 1854 are common intertidal snails, many of which lead an amphibious existence in muddy, estuarine habiats. Largely confined to tropical and subtropical regions, they are conspicuous members of the fauna of mangrove swamps and salt marshes where they graze on detritus and microalgae. The family represents the estuarine radiation of the superfamily Cerithiacea and is morphologically similar to the large family Cerithiidae Fleming, 1828, which has exploited intertidal and shallow water marine habitats. Both groups tend to be confined to shallow water or intertidal zones and both have an impressive fossil record extending back to the late Cretaceous. Both the Potamididae and Cerithiidae underwent an extensive adaptive radiation in the Tethys Sea during the early Tertiary.

The family Potamididae comprises numerous genera of many diverse shell forms. Members of some genera, such as *Telescopium* Montfort, 1910, *Pyrazus* Montfort, 1910 and *Terebralia* Swainson, 1840, are relatively large snails. Other genera, such as *Batillaria* Benson, 1842 and *Cerithidea* Swainson, 1840, comprise numerous species of smaller snails. Most species are common and occur in large, sometimes enormous, populations that are easily sampled. Although the ecology of a number of species of various genera has been studied, little is known of their comparative anatomies or life histories and almost all generic and higher taxa are defined on shell and radular characters alone. Clearly, the higher taxa assigned to the family Potamididae have not received adequate systematic attention and remain poorly defined.

The family Potamididae is divided into two subfamilies, the Potamidinae and the Batillariinae (Thiele, 1929; Wenz, 1938). Members of the latter live mainly in temperate or subtropical areas while the former group is largely tropical in distribution. The subfamilies are traditionally distinguished by radular structures: the Batillariinae have cusps on the lower basal plate of the rachidian tooth while the Potamidinae lack this feature. Bishop (1987:76) found that the Potamidinae exhibited a greater degree of heterogeneity of both shell and radular characters than the Batillariinae and suggested

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that the former group was probably polyphyletic. Within the subfamily Potamidinae, the genus *Cerithidea* is the largest group.

The main purpose of this paper is to establish reliable morphological characters defining the taxa *Cerithidea* Swainson, 1840, and the three subgenera comprising it: *Cerithidea* s.s., *Cerithideopsis* Thiele, 1929, and *Cerithideopsilla* Thiele, 1929. This allows establishment of homologies and development of hypotheses about polarization of character states and construction of phylogenetic trees. To this end, I describe in detail the shell, radula, soft parts and spawn of selected *Cerithidea* species, concentrating on *Cerithidea scalariformis* (Say, 1825), but employing characters noted in other species. This paper begins with a detailed description of *Cerithidea scalariformis* followed by an account of its reproductive biology and ecology. A discussion incorporates comparative observations on the anatomy, reproduction, growth and ecology of other *Cerithidea* species. Systematic conclusions based on these observations, the fossil record and cladistic analysis of the characters follow.

MATERIALS AND METHODS

I studied *Cerithidea scalariformis* at the Smithsonian Marine Station at Ft. Pierce, Florida. This facility is located on the mid-eastern coast of Florida along the Indian River estuary. A large population was studied on various occasions over a three year period at Big Starvation Cove, across the Indian River from Link Port, Florida (voucher specimens USNM 806783). Although observations were not continuous, I was able to determine the reproductive biology and growth of this population and had adequate material for dissection and morphometric studies. Morphological studies and field observations were also made on *Cerithidea californica* (Haldeman, 1840) from Anaheim Bay, Los Angeles, California. In addition, I briefly observed populations of *Cerithidea costata* (da Costa, 1778) at New Port Richie, Florida (USNM 770694), and *C. pliculosa* (Menke, 1820) at El Zacatal, Laguna de Terminos, Campeche, Mexico (USNM 702904). Preserved material of *C. obtusa* (Lamarck, 1822) [USNM 777233, Rayong, Thailand], *C. quadrata* Sowerby, 1855 [USNM 777651, Satahib Chonburi, Thailand], *C. decollata* (Linnaeus, 1767) [USNM 63348, Ambataloaka, SW Nossi Bé, Madagascar], *C. cingulata* (Gmelin, 1807) [USNM 776696, Ban Ampoe, Satahip, Chonburi, Thailand; USNM 794168, Bais Bay, Negros Oriental, Philippines], and *C. montagnei* (Orbigny, 1841) [USNM 809164, Barra de Navidad, Jalisco, Mexico] from collections in the USNM was dissected for comparative purposes.

Dissections of living material were made using animals relaxed in a 7.5% magnesium chloride solution. Carmine particles were used to determine ciliary tracts and an aqueous solution of methylene blue was used to enhance glandular and nervous tissues in preserved specimens. Animals were fixed in Bouin's fluid, embedded in paraffin, sectioned at 9 μm, stained with Harris' Hematoxylin and counterstained with eosin Y. Scanning electron micrographs were taken on a Mark II Stereoscan Microscope. Eggs and embryos were maintained in sea water in covered petri dishes.

Random samples of the Big Starvation Cove population of *Cerithidea scalariformis* were taken throughout a year-long period in 1980–81. Shell lengths were measured and histograms made to determine the growth pattern of the population. Dissection of various age classes of snails were also made to follow reproductive tract ontogeny.

A cladistic analysis of the *Cerithidea* subgenera using 19 characters comprising 38 character states was made using the Wagner 78 algorithm (Farris, 1970; Wiley, 1981:178–192). This program produced computer generated cladograms that were tested against the fossil record, developmental data, and ecological information to derive a phylogenetic classification incorporating all available evidence. Throughout this analysis I endeavored to discount results derived solely by rigid adherence to methodology but attempted to produce a classification based upon all the information at hand. Polarity was established primarily by out group comparison of presumed homologous structures derived from shell, animal and radula. *Batillaria* was chosen as the out group because it was the only other potamidid group that was relatively well known. Characters and scoring of character states are presented in Table 5, and a more detailed account of the cladistic methodology is presented in the "Systematic Conclusions" section of this paper.

RESULTS

BIOLOGY OF *CERITHIDEA SCALARIFORMIS*

Cerithidea scalariformis (Say, 1825) is a common, estuarine, amphibious snail that lives along the edges of muddy tidal creeks in salt marsh and mangrove habitats. It is assigned to the subfamily Potamidinae H. and A. Adams, 1854, genus *Cerithidea* Swainson, 1840, subgenus *Cerithideopsis* Thiele, 1929. Its geographic range is Georgia, both coasts of Florida, and Cuba.

MORPHOLOGY: *Shell description* (Fig. 1, A–B, E–G). Shell turreted, elongate, thin, comprising about 12 inflated whorls, ranging from 18–30 mm in length and 7–10.5 mm in width, having apical angle of 25 degrees. Shells of females significantly larger than males (see Table 1). Embryonic whorls (protoconch one) smooth, bulbous, forming about one and a half whorls (Fig. 1, E–G). Juvenile (post-embryonic) whorls have axial riblets and are angular in outline due to dominant median spiral cord that diminishes in size and disappears on fifth whorl. Teleoconch (adult) whorls each sculptured with about 26 concave axial ribs and a single, basal, spiral cord at the suture. Axial ribs become more numerous on penultimate and body whorls. Body whorl with about five strong, spiral cords on its lower half. Early whorls usually eroded or decollate in adults (Fig. 3, D). Aperture nearly one-fifth the length of the shell, circular; columella

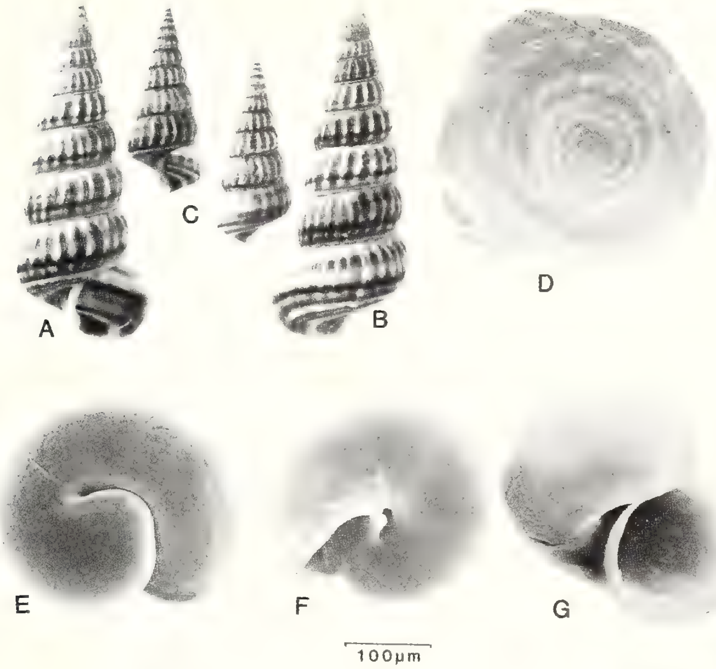

Fig. 1. *Cerithidea scalariformis* from Big Starvation Cove, Indian River, Ft. Pierce, Florida. **A,B)** Shell of adult female (28.5 mm length); **C)** Immature snail lacking thickened outer lip (10.11 mm length); **D)** Scanning electron micrograph of operculum showing central nucleus and multispiral growth lines (2.8 mm diameter); **E–G)** Scanning electron micrographs of shells of newly hatched snails showing aspects of protoconch and aperture.

Table 1. Sexual dimorphism in the shell of *Cerithidea scalariformis* ("t" test, df = 2, ** = $p < 0.01$).

Statistic		$\bar{x}$	sd	Range	n
shell length	females	24.39	2.26	22–30	12
t = 4.13**	males	20.55	1.48	18–22.1	10
shell width	females	8.95	0.68	8–10.5	12
t = 3.25**	males	7.78	0.49	7–8.4	10
aperture length	females	6.7	0.51	5.5–7.2	12
t = 5.46**	males	5.5	0.53	4.7–6.2	10
aperture width	females	5.90	0.42	5–6.4	12
t = 3.82**	males	5.25	0.36	4.5–5.6	10

concave; no anal canal present. Outer lip smooth, convex, slightly flared and with thickened varix at its edge. Anterior siphonal canal reduced; base of outer lip broady depressed in this area. Suture incised. Shell color brownish with tan base. Thick spiral brown band on base of each whorl and several thinner, spiral, brown bands present on mid-portion of whorls. Axial ribs white.

Operculum (Fig. 1,D). Operculum corneous, thin, circular and multispiral with central nucleus. Periphery of operculum flared, slightly reflected when animal withdrawn into shell aperture, providing complete closure.

Animal; External features (Fig. 2, B–C). When removed from the shell, animal has about six whorls. Base color of head-foot cream-yellow, flecked and striped with brown. Foot whitish and mantle bright green. Head large with long, extensible, shovel-shaped snout having transverse wrinkles and a bilobed tip. Cephalic tentacles moderately long, bearing single black eye on outer edge of peduncular stalk. Foot long, crescent shaped at front and tapering posteriorly. Anterior pedal gland a thin, deep furrow at edge of propodium, ending at mesopodium. Sole of foot with slight longitudinal folds. Median right side of foot of females has deeply embedded, ciliated groove leading from genital opening to large whitish bulbous ovipositor lying dorsal to groove (Figure 2, B, *ovp*). Males lack groove. Mantle edge turned slightly back, smooth and yellow. Mantle thin, pigmented green. Major mantle organs visible through mantle wall. Long, narrow, one-lobed kidney of green-white color present. Gonads overlay brown digestive gland on anterior of each upper whorl. Inhalant siphon on left mantle edge bears single eye, black at center, covered with round lens and surrounded by orange pigment cup. When animal withdraws into shell, pallial eye may be protruded at anterior siphonal canal of

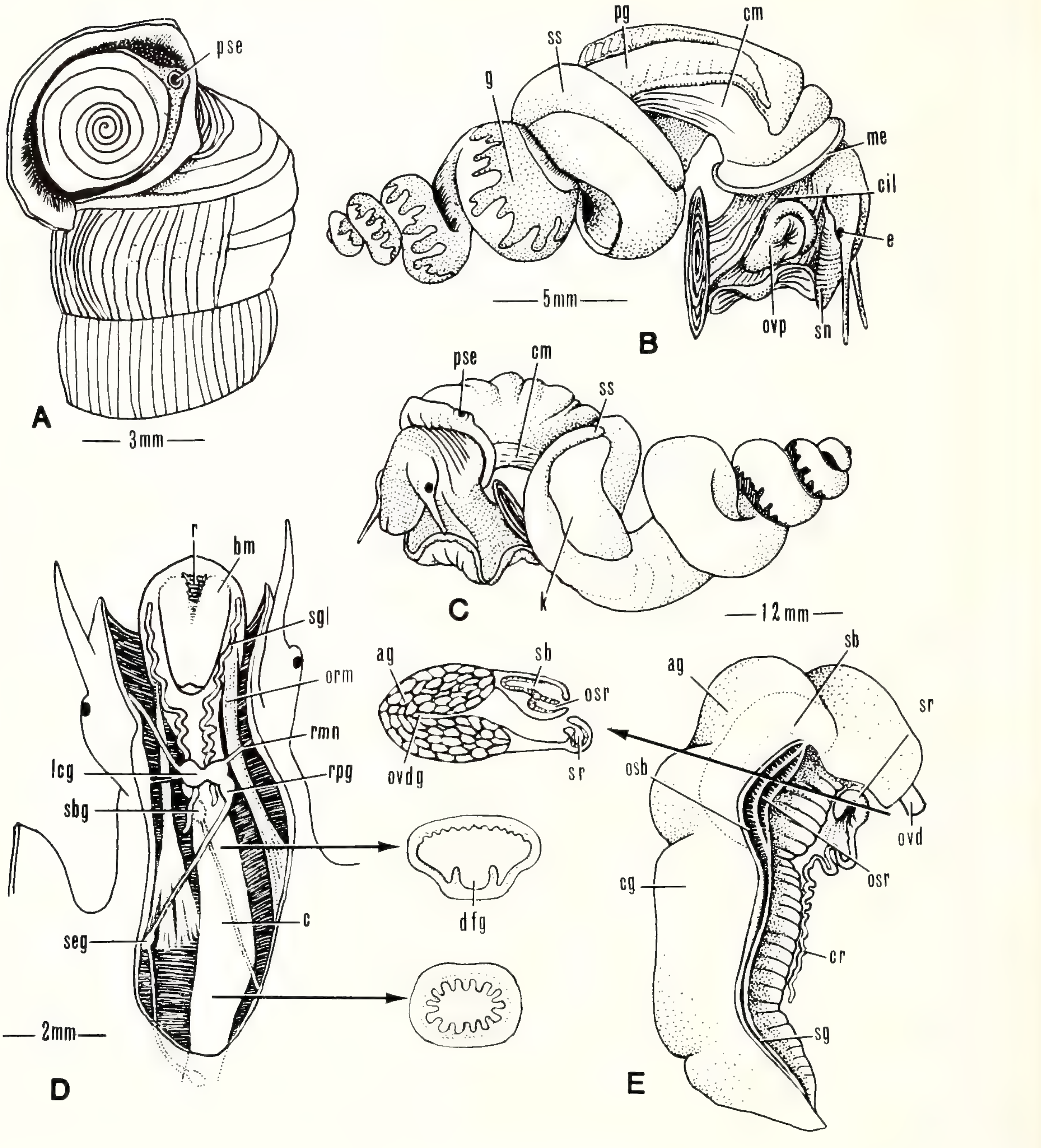
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Fig. 2. A) View of shell aperture showing retracted animal of *Cerithidea scalariformis* with pallial eye exposed in anterior canal of shell; **B)** Female removed from shell; **C)** Male, showing pallial eye at mantle edge; **D)** Diagrammatic representation of anterior alimentary tract and nerve ring exposed by dorsal longitudinal cut with sections through mid and posterior esophagus (large arrows); **E)** Female pallial oviduct showing major anatomical features and cross section through seminal receptacle and spermatophore bursa (large arrow). Abbreviations: *ag*, albumen gland; *bm*, buccal mass; *c*, crop; *cg*, capsule gland; *cil*, ciliated groove; *cm*, columellar muscle; *dfg*, dorsal food groove; *e*, eye; *g*, gonad; *k*, kidney; *lcg*, left cerebral ganglion; *me*, mantle edge; *orm*, odontophore retractor muscle; *osb*, opening to spermatophore bursa; *osr*, opening to seminal receptacle; *ovd*, oviduct; *ovdg*, oviducal groove; *ovp*, ovipositor; *pg*, pallial gonoduct; *pse*, pallial siphonal eye; *r*, radula; *rmn*, right mantle nerve; *rpg*, right pleural ganglion; *sb*, spermatophore bursa; *sbg*, subesophageal ganglion; *seg*, supraesophageal ganglion; *sg*, sperm gutter; *sgl*, salivary gland; *sn*, snout; *sr*, seminal receptacle; *ss*, style sac.

shell under opercular edge (Fig. 2, A, *pse*). Portion of operculum covering pallial eye somewhat transparent.

Pallial siphonal eye (Fig. 3, A–C). The pallial eye, located at the edge of the inner surface of the inhalant siphon (Fig. 2, A,C, *pse*), is surronded by pigmented epithelium. The outer area is bright orange but black pigment surrounds the lens. The pigmented epithelium appears to consist of pigment and sensory cells. The pigment cells (Fig. 3, C, *pc*) have darkly stained granules concentrated at the epithelial surface. A thin layer of tiny cells derived from mantle epithelium forms the cornea over the lens. The corneal cells extend around the lens and appear to be joined with the mantle epithelium. The lens is ovate and comprised of a single layer of very long, narrow, rod-like cells (Fig. 3, C, *l*) that stain red in eosin. The basal nuclei of the lens cells stain more darkly and are separated from the vitreous body by a thin basement membrane. The portion of the lens cells nearest the surface corneal layer stains a light pink color. Beneath the lens is a clear, large, vitreous body (Fig. 3, C, *vh*) which stains lightly and does not have a continuous cell structure. There are faint traces of disorganized cell walls and a few isolated, large, vacuolated cells with tiny dark nuclei scattered throughout the vitreous body. These are like the detached sensory cells depicted by Pflugfelder (1930:281) in the vitreous body of the pallial eye of *Cerithidea obtusa*. The entire structure of the vitreous body is disorganized and is difficult to interpret. The retina (Figs. 2–3, B, C, *rc*) seems to derive from the epithelium which has sunk in from the surface and lies beneath the vitreous body. It is characterized by a discrete layer of irregularly arranged, rounded sensory cells, each containing a light staining body that fills the cell and bears a darkly stained nucleus. Nuclei are concentrated at the bases of the cells adjacent to the vitreous body. Beneath the retina lies a thicker layer of larger, irregularly arranged pigment cells, most of which are granulose interiorly. Some of the cells stain weakly with hematoxolin. The function of all the cells in this area was not determined, but most are probably sensory cells of the retina because nerve fibers appear to penetrate the pigment cells and terminate in this loosely organized portion beneath the retina. The entire retinal area lies within tissue composed of elongated, darkly staining cells that form the pigment cup (Fig. 3, C, *pc*). Pigment cells contain tiny dark granules and are irregulary dispersed beneath the retina and sensory cells. A sensory nerve (Fig. 3, B, *n*) emerges from a ganglion in the pallial siphon and extends to the eye where it divides into smaller fibers that appear to penetrate the pigment cup. The manner of innervation of the retina was not discerned.

Mantle cavity and associated organs (Fig. 2, D). The mantle edge is slightly thickened at the undersurface of the inhalant siphon. The mantle skirt in this area is weakly pustulate anterior to the ctenidium and hypobranchial gland. The mantle cavity occupies about three-fourths of a body whorl and is relatively spacious but not particulary deep. The osphradium (Fig. 3, A) is a simple thin, black ridge bearing basal cilia on both sides that begins distally a few millimeters behind the mantle edge adjacent to the ctenidium. It is not quite one-half the length of the ctenidium and terminates at the mid point of the ctenidial axis. The monopectinate ctenidium is gray, broad and low, and extends back into the mantle cavity ending at the pericardium. The gill filaments extend across the mantle roof and lack supporting rods. The hypobranchial gland is a thin sheet of weak, transversely folded tissue that secretes great amounts of mucus. It is not well-defined and extends over the rectum where it assumes a white, fuzzy appearance and is heavily ciliated. The rectum is a wide, spacious tube through which may be seen numerous rod-like fecal pellets. The pallial gonoducts are open slit tubes that extend the length of the mantle cavity. They are wide and glandular in both sexes but particularly so in females. Males are aphallate.

Alimentary system (Fig. 2, D). Mouth lies between lobes of snout tip. Jaws (about 0.8 mm long) very thin, nearly transparent, composed of microscopic scales arranged in shingle-like pattern. Buccal mass moderate in size and taeniglossate radula (Fig. 3, H–J) short in relation to shell length, comprising about 98 rows of teeth and one-ninth length of shell. Rachidian tooth, although asymmetrical, (Fig. 3, J) somewhat pentagonal in shape and concave dorsally. Cutting edge bears five cusps: a long, central, pointed one flanked on each side by pair of smaller, pointed denticles. Basal plate of rachidian tooth flat and with central basal projection (glabrella). Lateral tooth (Fig. 3, I) rhomboidal with long, tapering lateral projection inserting onto basal radular membrane. Top of lateral tooth convex, cutting edge bearing four to five cusps: a small pointed denticle, a large elongate cusp and two to three smaller cusps, respectively. Beneath cutting edge of lateral tooth the basal plate is flat and squarish. Marginal teeth (Fig. 3, H) long, curving and spatulate at tips. Marginals fold over central portion of radular ribbon when not in use. Tips of inner marginal tooth serrated with four broad, nearly fused, cusps; outer marginal tooth has five small pointed cusps.

A pair of large odontophore retractor muscles (Fig. 2, D, *orm*) extends from their insertion on the posterior ventral portion of the buccal mass to each side of the wall of the cephalic cavity, posterior to the nerve ring. The radula sac originates at the ventral-median portion of the buccal mass and extends dorsally. The paired salivary glands (Fig. 2, D, *sgl*) are thick, convoluted tubes that originate slightly behind the nerve ring although they lie mostly anterior to it. The salivary glands taper at their proximal ends, pass through the nerve ring (Fig. 2, D) and each empties into the anterior lateral portion of the buccal cavity. The anterior esophagus has a typical dorsal food channel that twists as it passes through the nerve ring. Posterior to the nerve ring is the large swollen "crop" portion of the esophagus (Fig. 2, D, *c*) encased in very thin tissue. There is no evidence of an esophageal gland. Sections of the midesophagus reveal a deep ventral food channel (Fig. 2, D, *dfg*) and several dorsal longitudinal folds. The food groove is gradually lost in the posterior esophagus (Fig. 2, D, 2) which, in section, has many longitudinal folds. The stomach is a large organ, about one and a half whorls long. The oesphagus opens into it mid-

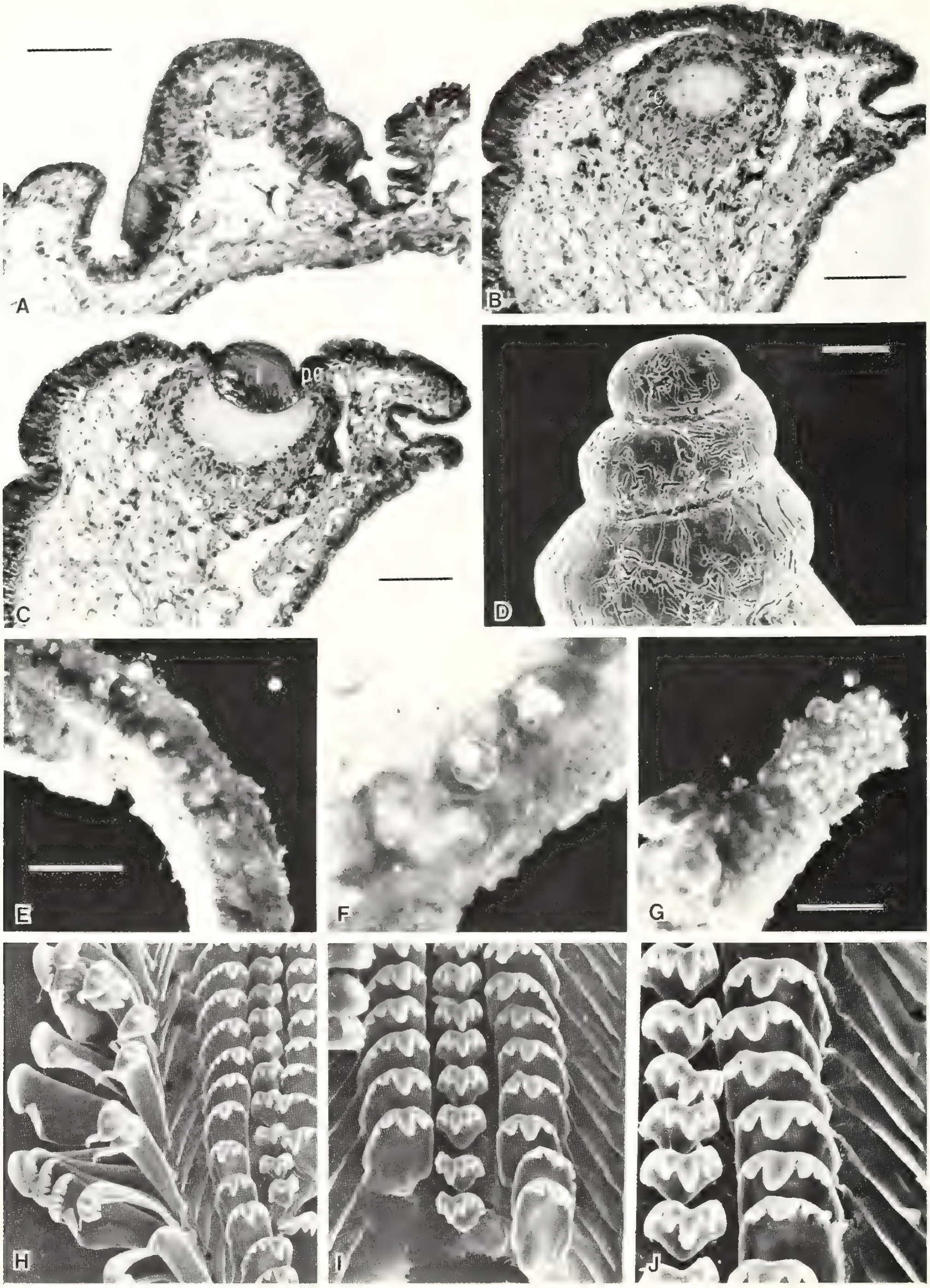

Fig. 3. *Cerithidea scalariformis* (exclusive of G). **A)** Histological section through osphradium showing basal cilia (*bc*), osphradial nerve (*on*) and blood vessel (*bv*) (bar = 0.05 mm); **B)** Histological section of edge of pallial eye showing vitreous humor (*vh*) surrounded by retinal cells (*rc*) and nerve fibers (*n*) (bar = 0.05 mm); **C)** Section through center of pallial eye showing cornea, lens (*l*), vitreous humor (*vh*), retinal (*rc*) and subretinal cells, pigment cells (*pc*) and optic nerve fibers (bar = 0.05 mm); **D)** Early whorls of juvenile snail showing etching of shell surface by fungus (bar = 0.5 mm); **E)** Strand of spawn mass of *Cerithidea scalariformis* showing sandy outer covering of jelly string and veliger stage embryos within individual egg capsules (bar = 2.5 mm); **F)** Detail of embryos in egg mass (capsule diameter 0.38 mm); **G)** Portion of egg mass of *Cerithidea californica* with detritus removed from one end to expose embryos within jelly string (bar = .25 mm); **H–J)** Scanning electron micrographs of *Cerithidea scalariformis* radula: **H)** Marginal teeth (note numerous cusps and wide flange on outer marginal tooth and larger, fewer cusps on tip of inner marginal tooth; **I)** Detail of lateral and rachidian teeth showing flat basal plate and long, lateral extension of lateral tooth; **J)** Detail of rachidian tooth showing cusps and basal plate.

ventrally and empties into a finely folded sorting area. A pad-like ridge lies between the esophagus opening and the two liver ducts. A prominent, cuticularized gastric shield is present as well as a very long style sac which bears an equally long crystalline style, nearly one-half the snail's length (about 10 mm in length in an average snail 22 mm long). The style sac may be clearly seen on the exterior of the animal through the mantle wall (Fig. 2, B,C, *ss*). The intestinal opening lies at the anterior ventral part of the stomach at the base of the style sac. A prominent ventral fold runs along the intestine to the mantle. This is the pellet compacting area. The pallial rectum widens and has a dorsal fold and numerous transverse internal folds that become almost leaflet-like. In section, this area appears to be glandular and may secrete additional mucus to bind fecal pellets together. This part of the intestine holds numerous rod-shaped fecal pellets, each about 1.4 mm long and composed of very fine detrital particles. The fecal pellets are arranged in stacks. The anus is papillate, slightly detached from mantle wall, and opens near the exhalant siphon at the right mantle edge. The lobate digestive gland is made up of numerous small ovate diverticula arranged in clusters like grapes. Each diverticulum is filled with small dark brown spherical bodies.

Nervous system (Fig. 2, D). *Cerithidea scalariformis* has an epiathroid nervous system that is somewhat loosely condensed. The RPG ratio as defiend by Davis *et al.* (1976:263; length of the pleuro-supraesophageal connective divided by the sum of the lengths of the supraesophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion), is 0.79 indicating a looser condition than those recorded for members of the Cerithiidae (0.59) but close to the 0.77 value recorded by *Batillaria minima* (see Houbrick, 1980a:138). The cerebral commissure is short, thick and the ganglia are almost fused to each other. The connectives between the cerebral and pleural ganglia are also short and thick. The subesophageal ganglion (Fig. 2, D, *seg*) is almost joined to the left pleural ganglion. The supraesophageal connective is very long and the supraesophageal ganglion sends out nerves that are connected to the long, left mantle nerve by a dialyneury. The pedal ganglia are deeply embedded in the muscular tissue of the foot. A pair of large statocysts is embedded adjacent to the posterior portion of the pedal ganglia. The visceral loop is very long and the visceral ganglion lies close to the base of the kidney and the posterior pallial gonoduct.

Reproductive system (Fig. 2, B,C,E). Sexes separate, pallial gonoducts open, forming slit tube that comprises outer (left) lamina and inner (right) lamina, which are fused to mantle wall overlying collumellar muscle. Males aphallate and produce spermatophores. Females tend to be larger than males (see Table 1) and have ovipositor in form of deep pit with lobe bordering it anteriorly (Fig. 2, B, *ovp*). Some snails are parasitized by trematodes with single-tailed cercaria. These individuals are difficult to sex because parasitized snails have reduced pallial gonoducts and tend to lose all secondary sexual characters. Parasitized snails are easily distinguished by the white color of their gonads due to the large numbers of sporocysts, rediae and metacercariae in the gonadal tissue.

Male reproductive tract. Males are distinguished from females by the lack of an ovipositor on the median right side of the foot and by their bright yellow testis. Adult males have smaller shells than females (see Table 1): some immature snails that lack a fully developed outer shell lip are males and have sperm in the vas deferens and vas efferens of the testis, but there is no evidence of protandry. The pallial gonoduct of males is composed of two thin laminae that internally bear many transverse, glandular folds. The distal portion of the pallial gonoduct is nearly transparent while the proximal third is white, thick and, in sections, more glandular. This is probably the prostate-spermatophore forming gland. The bright yellow testis overlies the digestive gland on the anterior portion of the upper whorls. Both eupyrene and multiflagellate apyrene sperm are present.

Female reproductive tract (Fig. 2, E). The female gonad is whitish-green. The pallial oviduct is a more complex structure than the gonoduct of the male. The oviducal groove (Fig. 2, E, *ovdg*), down which fertilized eggs move, lies between the two laminae that are fused to the mantle wall. Both inner and outer lamina are highly glandular and internally bear thick transverse folds along their entire lengths. The outer lamina (left) is thick but simple at its distal end (Fig. 2, E). The free edge of the outer lamina has a sperm collecting gutter (Fig. 2, E, *sg*) that begins distally and widens as it approaches the proximal third of the lamina. Here it bifurcates into a left bursa (Fig. 2, E, *sb*) that accommodates spermatophores and a right chamber (Fig. 2, E, *osr*) that may be a seminal receptacle or a storage area for sperm. Both the bursa and seminal receptacle are internally lined with tiny longitudinal folds and are heavily ciliated. The proximal end of the pallial oviduct is an opaque white color and functions as the albumen gland (Fig. 2, E, *ag*). At the edge of the proximal part of the inner lamina is a folded, flap-like, highly ciliated tissue that folds like an envelope and contains numerous oriented sperm. This structure is the seminal receptacle (Fig. 2, E, *sr*) and lies adjacent to and fits into the opening on the edge of the outer lamina which houses the bursa and seminal chamber. Together, these structures form a working unit that functions as the seminal recepacle but their exact functional relationship to each other as regards fertilization of eggs was not determined. The portion of the pallial oviduct that houses the bursa and seminal receptacle is not as opaque as the albumin gland which lies posterior to it. The central portion of the pallial oviduct is highly glandular, thick and is an opaque, white color. This is probably the capsule gland (Fig. 2, E, *cg*).

Excretory and Circulatory systems. The kidney (Fig. 2, C, *k*) is a long, relatively narrow, greenish-white organ easily seen on the exterior of the animal. It is one-lobed and bears both a renopericardial duct and a kidney opening. The heart and circulatory system are typically monotocardian.

REPRODUCTION AND GROWTH: The Potamididiae are aphallate, as are all marine cerithiaceans, and although pairing was not observed, it probably occurs as described in *Cerithium* Bruguière and *Modulus* Linnaeus (Houbrick, 1973; 1980a), with transfer of spermatophores from male to female via the siphons. Spermatophores are held in the spermatophore bursa (Fig. 2, E, *sb*), which may be homologous with the bursa copulatrix of phallate prosobranchs. After spermatophore disintegration, freed sperm move to the seminal receptacle by ciliary tracts in the laminae of the pallial oviduct. The exact mechanism of this transfer is unknown. The seminal receptacle lies at the distal end of the inner lamina adjacent to the opening of the ovicuct into the pallial cavity. Eggs are fertilized, pass through the albumin and capsule glands and emerge as long jelly strings. The mechanism of jelly string formation and oviposition were not observed, but the ovipositor is connected to the genital opening by a ciliated groove (Fig. 2, B, *cil*). In section, it is comprised of highly glandular mucous cells as determined by cytomorphology and probably secretes the jelly as well as molding the string as it is cemented to the substrate.

Spawn of *Cerithidea scalariformis* (Fig. 3, E–F) was deposited in the field from late September through November. Hatchlings were found in the field during these same months over a three year period of sampling, indicating that the spawning period for this species is during the autumn. A few cases of spawning were noted outside this period but these appear to be random and insignificant. Development is direct and hatching occurs about three weeks after deposition of spawn. The bulbous embryonic shell of few whorls and its smooth outer lip (Fig. 1, E–G) are typical of prosobranchs with direct development. The narrow geographic range and patchy distribution of populations indicate that this species is a poor larval disperser.

Spawn (Fig. 3). *Cerithidea scalariformis* deposits long, detritus covered jelly strings (Fig. 3, E–F) about 51 mm long and 1.13 mm in diameter. Jelly strings are transparent and sticky when first emerging from the female but the surface becomes covered with detritus and is parchment-like after exposure to water. Spawn masses are laid on bark, decaying wood and leaves and are cryptic in the natural habitat. Each jelly string is round in cross section but flat where it is attached to the substratum. Spawn masses vary in length and configuration and contain about 350 eggs per mass. Egg capsules are transparent, about 0.37 mm in diameter and contain albumin and a single egg about 0.28 mm in diameter (see Table 2 for spawn statistics). Egg capsules are arranged in a loose spiral within the jelly string and are packed about three deep in cross section. Each capsule is embedded in a sticky jelly matrix and separated from adjacent capsules by a clear, thin walled partition (Fig. 3, F). No nurse eggs are present. The bright green eggs undergo cleavage quckly after deposition. Early embryonic stages are also green but become lighter colored by the time the veliger stage is reached (about five days after deposition). The green pigment is then concentrated in the yolk and digestive gland. Veliger stage embryos rotate slowly within their albumin filled capsules. They have eye spots, small velar lobes with short cilia and a large larval shell typical of direct developing larvae. The larvae are very similar to what I have described for *Cerithium lutosum* (Menke), *Cerithium muscarum* Say and *Modulus modulus* (Houbrick 1973, 1974). Larval shells (Fig. 1, E–G) have a brownish-red cast around the lip margin and columella and are about 0.31 mm in diameter. Hatching occurs 18–22 days after deposition. Hachlings retain the velar lobes for a day or two but tend to crawl on the substratum using velar cilia only occasionally. No planktonic stage or swimming was observed. Hatchlings undergo rapid metamorphosis and become tiny snails within one to two days.

Table 2. Parameters of *Cerithidea scalariformis* spawn (measurements in mm).

Statistic	x̄	Range
length (n=4)	50.25	40–67
width (n=4)	1.11	1.0–1.4
no. eggs/mass (n=4)	372.5	276–502
capsule diameter (n=5)	0.36	0.35–0.38
embryo diameter (n=5)	0.28	0.28

Table 3. Shell length statistics of *Cerithidea scalariformis* from transect of tidal creek (3 ⅒ meter square samples) in January.

	n	Range	x̄	sd
HWM	59	3.57–22.80	11.22	7.05
MWM	246	2.08–21.8	5.64	2.67
LWM	142	1.20– 7.60	4.31	1.43

Growth. Growth is rapid: thousands of immature snails ranging in length from 1.1–13.0 mm appeared in the field four to five weeks after hatching and in greatest numbers during October and November. There are several cohorts of young due to the extended spawning period, direct development, and rapid growth but a single large cohort comprising all of these smaller groups is clearly discernable (see Fig. 4). Growth continues throughout the winter and by late January millions of subadults, from 2–8 mm in length, appear in the tidal creeks while the larger, older adults begin to die. Most adults had badly eroded shells and were heavily infested with trematode parasites. Immature snails tend to stay in the water where they crawl in the flocculant detritus, while adults are along creek banks or well above the water on plants (see Table 3). In general, adults tend to be amphibious and only occasionally crawl in water. Three ⅒ m^2 samples taken in a tidal creek at the high, mid and low tidal marks clearly demonstrated this segregation of age classes (Table 3).

By early spring, young snails were about half grown but not sexually mature. A few young males were detected but none were producing sperm. Several females showed signs of early egg production but none of these had fully developed ovipositors and their pallial oviducts were largely undifferentiated. The older generation of adults was almost completely gone at this time. Older snails were easily recog-

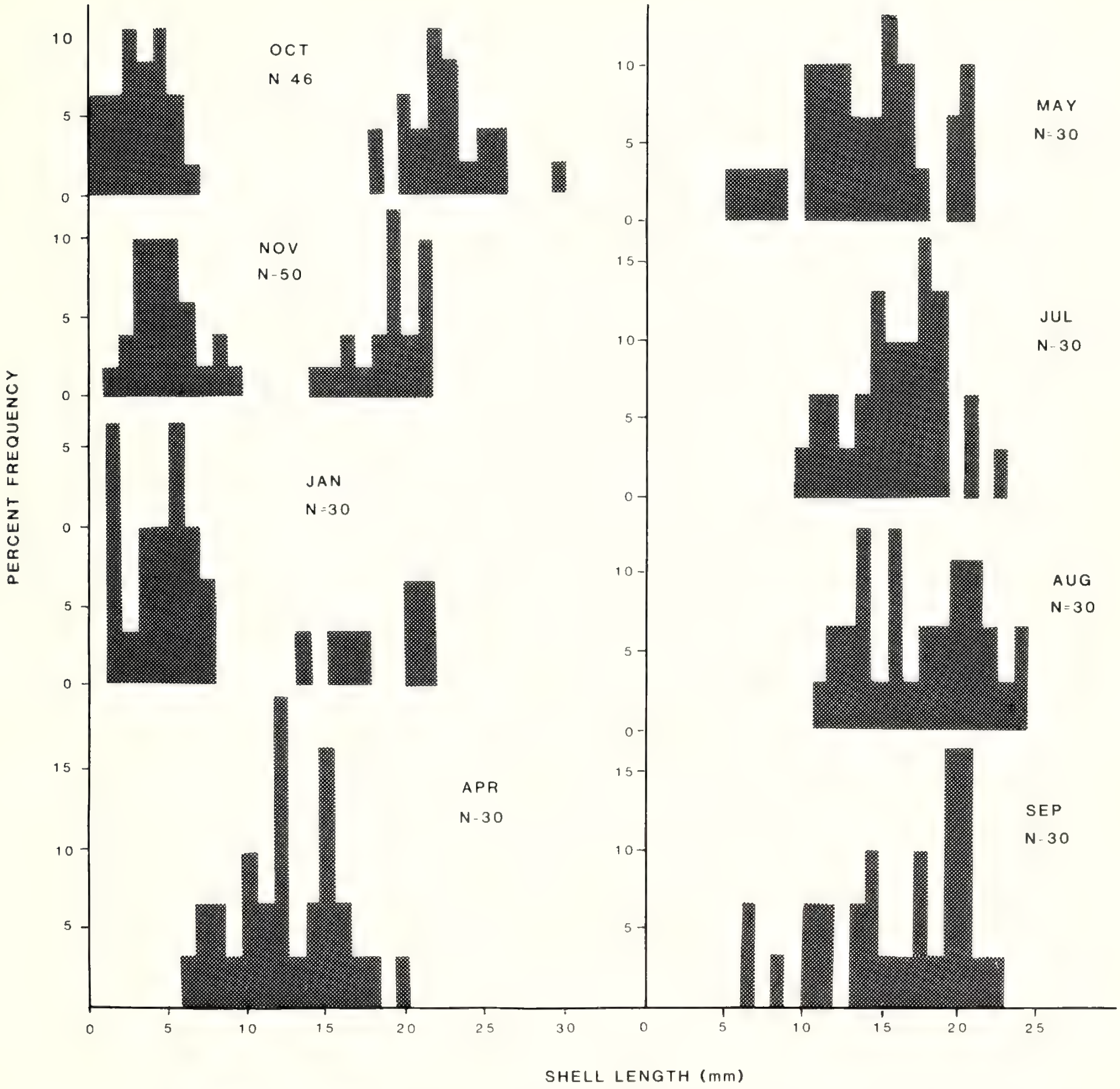

Fig. 4. Monthly percent length-frequency histograms of shells of *Cerithidea scalariformis* from Big Starvation Cove, Indian River, Ft. Pierce, Florida, covering one reproductive year, 1980–81.

nized by their badly eroded, chalky appearance. Monthly samples show that the new cohort achieves adult size and sexual maturity by early summer but the outer shell lips of these individuals have not yet become completely thickened. In August and September, most snails had achieved reproductive maturity and had thickened outer shell lips. Figure 4 illustrates growth over a year's period. It appears that adults live from one to two years.

HABITS AND HABITATS: *Cerithidea scalariformis* lives on muddy-sandy substrata in intertidal and supratidal estuarine habitats. The Big Starvation Cove population occurs along the banks and in shallow tidal creeks created by a mosquito impoundment area in a mangrove swamp along the Indian River. This is a somewhat artificial habitat subject to deliberate draining and flooding, but snails are exceedingly abundant here, numbering in the millions and comprising two size classes during the winter: large adult snails and juveniles of several size groups. These groups represent the adult reproductive population and its progeny. Although most snails are immersed in water during very high tides, adults tend to stay above the high water mark and may be found almost a meter above the high tide zone where they lie beneath or crawl up the vegetation bordering the water. Climbing response to escape immersion and predators as recorded in other *Cerithidea* species such as *Cerithidea* *decollata* (Linnaeus) (Cockcroft and Forbes, 1981b:8; Berry, 1972) and *Cerithidea obtusata* (Lamarck) (Sasekumar, 1974) is less pronounced in *Cerithidea scalariformis*. Normally, only a few snails climb vegetation although when the area is completely flooded most adults climb on *Salicornia* and mangroves just above the water level. Haros (1976) made the same observation on the population of *Cerithidea scalariformis* he studied and suggested that the climbing response is not strongly selected for. The dominant plant along the banks of the tidal creeks with which the *Cerithidea* population is associated is *Salicornia*. *Cerithidea scalariformis* had a wide tolerance to temperature, salinity and desiccation. Salinity is normally 33‰ but varies considerably during the year due to periods of drought and heavy rainfall. The entire site is rich in detritus and microalgae that form a flocculent mass at the water-substratum interface. Temperatures at the substratum surface vary considerably with season and exposure to the sun. Winter frosts may occur and extremely high temperatures are attained in the summer sun. Tidal levels fluctuate from 50 cm to 0.5 m depth and may be heavly influenced by rainfall. Larger snails tend to follow the tides while juveniles are more likely to be permanently immersed in the tidal creek where sediments and detrital particles are finer. Tidal creeks range in width from 1–3 m and have an average depth of about 50 cm. During low tides the creeks may be nearly dry exposing up to three meters of bank. At these periods, juveniles and some adults remain partially buried in the detritus. When the area is flooded by exceptional high tides, snails disperse everywhere.

I found no evidence of predation such as drilled or crab-cracked shells. Many wading birds, raccoons and opossums occur at the site but none were observed preying on *Cerithidea*. In May, many of the younger, subadult snails had the tips of their tentacles bitten off suggesting killifish predation. With the exception of *Uca*, no crabs were ever observed in the tidal creeks.

COMPARISON WITH OTHER CERITHIDEA TAXA

COMPARATIVE ANATOMY: The most thorough anatomical studies on *Cerithidea* are those on *C. californica* by Bright (1958) and Driscoll (1972), the latter writer concentrating on the alimentary tract. Aside from a few differences such as the structure of the pallial eye, the basic morphology of *C. scalariformis* and *C. californica* is similar, indicating a close relationship. However, species of other subgenera may differ considerably in the morphology of some organ systems, such as the respiratory, alimentary, and reproductive tracts.

Externally, *Cerithidea* females may be distinguished by the presence of a distinct, bulbous ovipositor on the right side of the foot (Fig. 2, B, *ovp*). Among the cerithiacea, a similar ovipositor occurs in *Cerithidea californica, Batillaria minima, Batillaria zonalis,* among *Cerithium* species (Cerithiidae) (Marcus and Marcus, 1964:507), and in *Modulus modulus* (Modulidae) (Houbrick, 1980a:121), and among the freshwater Melanopsidae, in *Melanopsis* and *Zemelanopsis* (Belgin, 1973). Bright (1960:13) apparently did not notice the ovipositor in *Cerithidea californica* because he stated that there was no sexual dimorphism in that species. He obviously misinterpreted the anatomical layout of the reproductive system and erroneously recorded a penis in males. His sections likewise indicate a total misunderstanding of the functional anatomy of the pallial gonoducts.

The outer lamina of the pallial oviduct of *Cerithidea* bears a long sperm collecting gutter (Fig. 2, E, *sg*) that widens in the proximal end to form the spermatophore bursa (Fig. 2, E, *sb*) which is possibly homologous with the bursa copulatrix of other prosobranchs, and a sperm pouch (Fig. 2, E, *sr*) that may function as a seminal receptacle. This is not unlike the condition in *Tympanotonus* (subfamily Potamidinae) described by Johansson (1956:160). According to his account, *Tympanotonus* has a ciliated ridge in the outer lamina but not a seminal receptacle. I believe the inner pouch depicted by him in the inner lamina of *Tympanotonus* is a seminal receptacle. *Cerithidea* also has another seminal receptacle in the proximal end of the inner lamina similar to the envelope-like receptacle found in the proximal inner lamina of *Modulus* (family Modulidae) (Houbrick, 1980a). A similar case of two seminal receptacles, one in each of the laminae, is described in *Bittium* (family Cerithiidae) by Fretter and Graham (1962:367). I have noted a seminal receptacle at the distal end of the inner lamina of *Cerithium nodulosum* (Houbrick, 1971). It appears that the seminal receptacle in the inner lamina is the larger of the two and that it may represent the "true" receptacle.

Pelseneer (1895:358) was the first to record the presence of a pallial eye in *Cerithidea*. He studied *C. obtusa* (Lamarck, 1822) and made sections of the pallial eye (1895:plate 15, figure 9). The structure of the eye described by Pelseneer (1895) closely resembles the eye of *C. scalariformis*. Pflugfelder (1930) made a more thorough study of the mantle eye of *C. obtusa* (cited as *Potamides obtusus*) in which he described the histology of the eye in detail. His sections are remarkably similar to those I made of *C. scalariformis*. The large nerve depicted by Pelseneer (1895:358) and Pflugfelder (1930:279) innervating the eye of *C. obtusa* and subdividing into branches which pass through the pigment cup and retina was not seen as clearly in my sections of *C. scalariformis*. Van Benthem Jutting (1956:435) was the only worker since Pfugfelder to note the presence of a pallial eye in *C. obtusa*.

The presence of a well-developed pallial siphonal eye has been overlooked in American *Cerithidea* species. Although significant anatomical and ecological work has been done on *C. californica,* no mention of its pallial eye occurs in the literature. I observed a pit-like pallial eye in *C. californica* from Anaheim Bay, Los Angeles, California. The mantle edge adjacent to the eye comprises several transparent bulb-like structures that are filled with white spherules. The function of these structures is unknown but they may gather and concentrate light. The pallial eye comprises a large pit bordered by darker pigment which, in cross section, lies in a dark orange pigment cup embedded in the mantle wall. Preserved specimens of *C. cingulata* (Gmelin) from

Thailand have a pit-like, small black pallial eye on the inner edge of the inhalant siphon. The outer surface bears small spherical bodies that appear to concentrate light and are similar to structures observed on the inner surface of the pallial siphon of *C. californica.* This kind of pallial eye differs from those observed in *C. scalariformis, C. costata,* and *C. pliculosa.* These species have a lens and cornea and are referred to the subgenus *Cerithideopsis* Thiele, 1929. I examined preserved specimens of *Cerithidea montagnei* (Orbigny) (= *reevianum* C. B. Adams) from the Canal Zone, Panama (LACM 70-64) and noted that this species also has a pallial eye similar to that of *C. californica.* I have also seen what appears to be a pit-like pallial eye in poorly preserved specimens of *Cerithidea quadrata* Sowerby. It appears likely that all *Cerithidea* species have some kind of pallial eye and that this organ is an important generic character.

Pflugfelder (1930:277) showed that the pallial eye of *Cerithidea obtusa* was located at the mantle edge and protruded into the anterior canal in living snails, which he claimed were only active at night. He observed the same kind of an eye in *Cerithidea quadrata* (cited as *Potamides quadratus*) but mentioned that he did not find pallial eyes in any other representatives of the "family of Cerithidea." It is unclear what he understood by this taxon, which has no validity. Pflugfelder probably meant the family Potamididae rather than the generic taxon *Cerithidea*, because all members of the genus *Cerithidea* appear to have pallial eyes.

The functional significance of the pallial eye in *Cerithidea* species is not clear. Presumably, this eye assists an amphibious snail to observe the immediate environment of the aperture prior to extruding the more vulnerable head-foot. Pflugfelder (1930) suggested that amphibious snails that are more active at night would have need of this eye to avoid predators during the day but it is unclear what these predators would be and how such an eye would help. Crabs are undoubtedly a danger to the *Cerithidea* species of Indo-Pacific swamps but do not appear to be a threat to *C. scalariformis.* The pallial eye may be more important to juvenile snails which live submerged in water where fish may nibble the extended cephalic tentacles.

The only other published account of a siphonal pallial eye in a potamidid is that of Johansson (1956) who described an eye located at the inner edge of the inhalant siphon of *Tympanotonus fuscatus* (Linnaeus). It consists of a black, bulging structure with a round white spot in the center. The pallial eye of *Tympanotonus* has a cornea of a single layer of high narrow cells with basal nuclei that form a weak lens. The pigment cup is penetrated by branches of the sensory nerve and the inner surface of the cup is covered with a retina. This eye differs from Pelseneer's (1895) description of the pallial eye of *Cerithidea obtusata* in that the retina of that species is penetrated by branches of the sensory nerve and the cornea does not form a lens. Some potamidids appear to have sensory structures other than eyes located in the same area of the mantle edge. For example, Pflugfelder (1977:248–249) mentioned that *Potamides telescopium* (probably *Terebralia palustris,* judging from the figure), a mangrove snail, had sensory areas on its mantle edge. Tenison-Woods (1888:175) recorded that the mantle edge of *Pyrazus ebininus* (Bruguière, 1792) [cited as *Cerithium ebininum*] was "studded with innumerable minute rounded bodies which refract light very brightly." He also noted rounded eye-like bodies in semilunar chambers with a distinct nerve supply in the same area and suggested that these are compound eyes. These observations need to be reconfirmed, preferably on living animals. If present, these are probably convergent structures similar to other pallial eyes such as those found in some cerithiids.

Among the Cerithiidae, I have described a pallial siphonal eye in *Gourmya gourmyi* (Crosse, 1861) (Houbrick, 1981b:5–6), which has numerous ocelli at the inner edge of the inhalant siphon. I have also observed a pit-like siphonal eye similar to that of *Cerithidea californica* in *Rhinoclavis (Proclava) kochii* (Philippi, 1848). I documented inhalant siphonal pigmented sensory areas in *Rhinoclavis* species (Houbrick, 1978) which I suggested might be specialized sensory or light sensitive organs. These structures all appear to be, at best, analogaous light sensory organs independently evolved from ectodermal epithelium. I agree with Johansson (1956:152) that they probably represent a convergent evolution. Nevertheless, their presence in members of different cerithiacean lineages may also suggest that they should be recognized as plesiomorphic characters. All examined *Cerithidea* species have pallial siphonal eyes located in the same area of the mantle. With the exception of *Tympanotonus,* all other potamidids lack this organ; thus, within the genus *Cerithidea*, pallial ocelli are probably homologous and useful as phylogenetic characters.

All *Cerithidea* species I examined have a low, broad ctenidium which extends the length of the mantle cavity. Individual filaments lack supporting rods. Pelseneer (1898) stated that *C. obtusa,* a species that lives almost entirely on dry land in the mangroves, has a reduced ctenidium and a network of blood vessels in the mantle roof. I have observed preserved specimens of *C. obtusa* and confirm his observation. This does not seem to be the only species with a reduced ctenidium. I found no trace of a ctenidium in *C. quadrata* Sowerby, but the specimens I examined were poorly preserved and the ctenidia may have been destroyed. Pelseneer (1895) suggested that the low, broad gill filaments seen in *Littorina* and some potamidid genera were an adaptation to terrestrial life and that *C. obtusa* was the most advanced form in this regard. Johansson (1956:150) supported Pelseneer's view and described a ctenidium similar to what I have recorded for *C. scalariformis* in *Tympanotonus fuscatus* (Linnaeus).

The osphradium in *Cerithidea* and all other potamidids examined is a simple ridge extending the length of the mantle cavity. It is reduced or absent in *Cerithidea*, s.s., species. It thus differs from the well developed bipectinate osphradium found in members of the Cerithiidae (Houbrick, 1974, 1978), Modulidae (Houbrick, 1980a), Diastomatidae (Houbrick, 1981b), and Campanilidae (Houbrick, 1981a). The potamidid osphradium is similar in structure to that of *Planaxis* (personal observation), *Littorina* and *Rissoa* (Johansson, 1956:150) and may be regarded as a primitive structure in this state. According to Pelseneer (1895), the osphradium of *Cerithidea obtusa* is absent, but I noted a tiny ridged structure in a poorly preserved specimen of that species suggesting that there is a vestigial osphradium and that Pelseneer's observation needs reconfirmation.

The radula differs among *Cerithidea* species, particularly in the configuration of the rachidian tooth and the outer lateral tooth (see Bishop, 1979:31, figures 3-1,d–f). The subgenera are partially defind by differences of the rachidian tooth. Cerff (1981:95–96) depicted scanning electron micrographs of *Cerithidea decollata* but showed only the cusps on the tips of the teeth. Cerff obviously misunderstood the entire configuration of the taenioglossate radula, because he described three lateral teeth and only one marginal tooth. His pictures indicate a spatulate, cuspless outer marginal tooth, an inner marginal tooth with rake-like denticles and a lateral tooth with six, relatively large, pointed denticles. He did not show the basal plate and glabrella of the rachidian tooth.

The rachidian tooth of members of the *Cerithideopsis* group as described and depicted herein is distinctive. It somewhat resembles that of *C. (Cerithideopsilla) cingulata* in general configuration but has fewer cusps. It differs considerably from the rachidian tooth of *Cerithidea* s.s. species such as *C. obtusa, C. decollata* and *C. kieneri* (see Bishop, 1979: figures). The rachidian tooth in true *Cerithidea* species is narrow, has an elongate, tear-shaped basal plate and bears a long, narrow central cusp.

One of the striking features of the alimentary system of *Cerithidea* is the long style sac. In all species I examined, the style sac projects anteriorly from the stomach to the pericardial sac (Fig. 2, C, *ss*). The style itself is nearly one-half the shell length in *C. scalariformis.* Driscoll (1972:384) suggested a functional relationship between style length and composition of ingested food. The rich, flocculent organic detritus ingested by *C. scalariformis* is extremely fine. The short radula, complex sorting area of the stomach and long style all indicate that the alimentary morphology of *Cerithidea* species is well adapted for feeding on fine particulate matter.

There seems to be minor variability in the layout of the nervous system of *Cerithidea* species and other potamidids. Bright (1958:16) does not show the dialyneury between the supraesophageal ganglion and the left mantle nerve that I record in *C. scalariformis.* Bouvier (1887:plate 7, figure 29) noted a similar dialyneury in *C. obtusa.* He also showed a zygoneury between the right pleural and subesophageal ganglia which I did not see in *C. scalariformis.* Bright (1958:10–11) made no mention of zygoneury in *C. californica.* Bouvier (1887) depicted other potamidids such as *Terebralia sulcata* (Bruguière) (cited as *Pyrazus sulcatus*) and *Pyrazus ebininus* (cited as *Potamides ebininus*) as having a similar zygoneury.

COMPARATIVE REPRODUCTIVE BIOLOGY: Both direct and indirect modes of development occur in *Cerithidea* species. It would appear that all *Cerithideopsis* species have direct (lecithotrophic) development. As mentioned above, *C. scalariformis* undergoes direct development and is a poor larval disperser with a limited geographic distribution. MacDonald (1967) made the same observation on *C. californica* although Race (1982) noted that the juvenile floating behavior indicates that it does have access to other habitats and is not completely restricted by lack of dispersal abilities. In contrast to *C. scalariformis,* which has a peak spawning period in September through November, MacDonald (1967) found mating pairs of *C. californica* common in May and spawn masses present from May to October with greatest abundance in July and August. The spawn of *C. californica* which I examined, consists of long, detritus-covered jelly strings within which are held the individual egg capsules. Jelly strings vary in length but five randomly collected strings had a mean length of 60 mm and a width of 2.5 mm. Jelly strands are tear shaped in cross section with the thin portion adhering to the substrate. Egg capsules are packed three to four deep within the jelly strands. There are about 540 egg capsules per spawn. An individual egg capsule is 0.4 mm in diameter and contains a single egg 0.28 mm in diameter. No nurse eggs are present. Advanced embryos were not observed. According to MacDonald (1967), the emerging veliger larvae settle immediately upon hatching, but Race (1982:344) stated that they undergo complete development without a planktonic stage. The eggs of *C. californica,* in mud covered strings, are laid on the substratum in the summer and fragile shelled juveniles emerge in high densities throughout this period. The latter observation is more than likely the correct one since it matches what I have seen in *C. scalariformis.* The protoconch is typical of a direct developing larva.

Habe (1955:204) described the egg masses of two species, *C. (Cerithideopsilla) djadjariensis* and *C. (Cerithidea) rhizophorarum.* The former species lays its eggs in a long jelly string 50–90 mm long and 3–3.5 mm wide. Habe's figure shows an elongate egg string filled with small eggs arranged in tight spirals. The spawn has an axial attachment surface, presumably flat. The small egg capsules (0.2 mm) and wide geographic dispersion of this species indicate a free swimming larval stage. *C. (Cerithidea) rhizophorarum* excavates a hole in the substratum and deposits its spawn in the bottom. The spawn mass consists of a sticky mass of jelly strings about 20 mm wide and 15 mm deep. Individual eggs are 0.35 mm in diameter, suggesting direct development. The spawn and larvae of *C. (Cerithideopsilla) fluviatilis* (Potiez and Michaud), which may be synonymous with *C. cingulata*, was described by Natarajan (1958:174–175), who showed that this species undergoes indirect development and hatches after a four day incubation period. He recorded an average of 4,800 eggs per spawn and small egg capsules 0.25 mm in diameter. Panikkar and Aiyar (1939) have also described the spawn of this species from Madras and Sadasivan (1948) gave an account of the growth rate, duration of the breeding season and age at maturity of this species. Amio (1963:304) depicted the spawn masses of *C.*

Table 4. Comparative measurements of *Cerithidea* spawn, eggs, and larvae (all measurements in mm and expressed as mean values calculated from present study and literature).

Species	Spawn length	Spawn width	No. eggs per mass	Capsule diameter	Embryo diameter	Citation
scalariformis	50.6	1.13	352.6	0.37	0.28	this study
californica	60	2.5	540	0.40	0.28	this study
rhizophorarum	20	14.5	—	0.35	—	Habe, 1955
djadjariensis	70	3.4	—	0.20	—	Habe, 1955
cingulata	80	—	—	0.21	0.11	Amio, 1963
fluviatilis	123	2.5	4,800	0.25	0.14	Natarajan, 1958

(Cerithidiopsilla) cingulata (Gmelin) and demonstrated indirect development with free swimming veliger larvae. The egg capsules are small (0.20–0.22 mm) and there is an incubation period of seven days prior to hatching.

A summary of the kinds of *Cerithidea* spawn, eggs and larvae is given in Table 4. From available published reports, it would appear that tree-dwelling and high tidal, amphibious species tend to have direct development and narrow, patchy geographic ranges while intertidal, widely dispersed species have free swimming veliger larvae. Direct and indirect modes of development have also been shown to occur in the cerithiid genus *Cerithium* (Houbrick, 1973, 1974).

A few published reports on growth patterns of *Cerithidea* species all show some basic similarities. There are differences in life spans, but adults do not increase their length by addition of new whorls once sexual maturity is attained but rather expand and strengthen their shell lips. As erosion of older shells increases, their decollate condition may become more acute and a pronounced reduction in length may occur. Life spans of direct developing snails are difficult to estimate when new subgroups constantly arise during the spawning season. On the basis of three years' observation, I suspect a life span in *C. scalariformis* of one to three years. However, my observations were cursory and not based on growth curves of marked cohorts. As seen in Figure 4, maximum growth rate occurs in juveniles (less than 10 mm). I rarely found adults that survived more than one to two years and these were obvious due to their badly eroded shells. Once adult stage is attained, there is little or no growth in shell length. The outer lip is strengthened and the shell color is lost due to erosion. MacDonald (1967) recorded maximum growth rates in *C. californica* 4–8 mm long and little or no growth in snails over 20 mm long. He observed that some snails do not grow every season and that varix counts underestimate an animal's true age. A maximum life span for *C. californica* was calculated to be seven years, considerably longer than what I estimate for *C. scalariformis*. Cockcroft and Forbes (1981a) found that growth in *C. (Cerithidea) decollata*, a tropical species, was also seasonal, showing an acceleration during summer months and a depression during winter. Summer growth decreases as size increases, while winter growth is relatively constant for all sizes. They estimated that it took three years for *C. decollata* to attain modal size (12–12.9 mm) and that maximum width was attained in excess of nine years. Snails of less than 10 mm width expanded and consolidated their shell lips rather than adding new whorls.

To my knowledge, no one has documented sexual dimorphism in the shells of *Cerithidea* and other potamidid species. Differences in the shell dimensions of males and females of *C. scalariformis* were highly significant (see Table 1), females having the larger shells. This is not surprising since the large pallial oviducts of females occupy more mantle cavity space than the smaller pallial gonoducts of males.

COMPARATIVE ECOLOGY: All *Cerithidea* species are surface animals that occur in dense aggregations and are easily collected because of their high intertidal habitat. The highest densities I observed in a population of *C. scalariformis* was 1,100 snails/m^2. MacDonald (1967) found *C. californica* to occur in densities as high as 13,800 snails/m^2.

I found few empty shells of *C. scalariformis* after death and disappearance of spawning adults. This species has a life span of about one to two years and it is surprising that so few dead shells occur. There are no hermit crabs to carry away shells in the Big Starvation Cove habitat and one rarely finds shells buried in the sediment. This is probably because shells of dead animals quickly become decalcified and break up. MacDonald (1967) observed the same phenomenon in *C. californica* populations and noted that dissolution of shells occurs before burial in the estuarine environments probably as a result of low pH.

A number of papers have been published on ecological zonation and tidal activity rhythms of this genus. Incidental notes about *Cerithidea* also occur in publications of mangrove ecology. Each of the three *Cerithidea* subgenera appears to have its own generalized habitat. This adds support to the subgeneric classification arrived at by analysis of morphological character states.

Cerithidea s.s. species appear to comprise a tree dwelling group. Brown (1971) found that *C. (Cerithidea) decollata* formed dense aggregations on mangrove tree trunks, between 1–2 meters from the ground, but that it fed for short periods on the mud surface of the substratum. He observed a general movement of the snails from the bases of trees to the mud after spring tides. This species, when not feeding, is attached to tree trunks at its aperture by dried mucus. Cockcroft and Forbes (1981b) showed that descent of *C. decollata* to the substratum was associated with feeding. They found that snails descended at low tide periods and ascended the trees before the following high tide and suggested that tree-climbing was a predator avoidance response. Berry (1972) also suggested that this species was primarily a tree-dweller that feeds on epiphytic algae and descends to browse on the mud when the mangrove is not flooded for several days. *Cerithidea (Cerithidea) quadrata* lives on mangrove roots but also occurs on the mud surface (Berry, 1963). According to Brandt (1974), this species feeds on algae growing at the roots and stems of mangroves. Likewise, *C. (Cerithidea) obtusa* occurs mainly on trees from 50–175 cm above the substratum (Houlihan, 1979; Sasekumar, 1970; 1974), but is occasionally found on the substratum. The *Cerithidea* s.s. group thus differs ecologically from other *Cerithidea* subgeneric taxa that do not spend appreciable time in the trees.

Members of the subgenus *Cerithideopsilla* live mainly on the substratum in intertidal mud flats. *Cerithidea (Cerithideopsilla) cingulata* is a wide-spread Indian Ocean species that is common on the surface of sandy flats in mangrove swamps or estuarine areas. Although Murty and Rao (1977) recorded that this species is abundant on the substratum and climbs mangrove roots with rising tides, it does not seem to be a tree dwelling species in the sense that *Cerithidea* s.s. species are. Basson *et al.* (1977) found dense aggregations of *C. cingulata* on the tidal flats of the western Persian Gulf. These populations were not associated with mangroves. Berry (1972) noted that *C. cingulata* was common on the soil surface of mangrove swamps in west Malaysia. In Singapore, Vohra (1970; 1971) noted that this species was not limited by particle size in its distribution but that it avoided clean, well-drained sand and was confined to regions of low salinity and pH. Vohra (1970) found no evidence for vertical migration with the tide but observed a seasonal migration, controlled perhaps by internal physiological rhythms. *Cerithidea cingulata* also showed segregation by size in relation to tidal levels, the largest, oldest individuals occurring upshore. My observations on size segregation of *C. scalariformis* are similar. Three other *Cerithideopsilla* species, *alata* (Philippi), *microptera* (Kiener) and *djadjariensis* (Martin), are reported by Brandt (1974) to live on mud flats.

Cerithideopsis species are all confined to the New World and the ecology of only a few is known. An account of the ecology of *C. (Cerithideopsis) scalariformis* has been presented earlier in this paper. *Cerithidea (Cerithideopsis) costata, C. (C.) californica,* and *C. (C.) pliculosa* all live primarily on muddy substratum and only occasionally climb trees or vegetation. This supratidal substratum group thus differs from *Cerithidea* s.s. species in ecology. The only thorough work on *C. scalariformis* of which I am aware is an unpublished master's thesis at Florida State University by Harlos (1976). He studied the environmental distribution of this species in a tidal marsh at Wakulla Beach, Apalachee Bay, Florida. His study site is not directly comparable to mine in that the Indian River site is a mosquito impoundment in which the water level is sometimes artificially regulated. Harlos found that *C. scalariformis* preferred a salinity substratum of 28‰ and that its vertical distribution along the shore can be predicted by substrata salinities. He concluded that predator influences in its distribution and behavior are insignificant. As in my study, Harlos found the highest densities of *Cerithidea* in the *Salicornia* zones. Predation was highest in small snails. Harlos (1976) found that snails under 8 mm in length were preyed upon by *Fundulus* fishes. Although I did not see this kind of predation, the only fish present in tidal creeeks at the Indian River site are *Fundulus* species. Harlos also observed the xanthid crab, *Panopeus herbstii* (Milne-Edwards), feeding on *Cerithidea* and suggested the clapper rail, *Rallus crepitans* (Gmelin), as another possible predator. I did not see any crabs in the tidal creeks at my study site, and although several kinds of wading birds are very common there, I never saw them feeding on snails. I found no evidence of predation such as drilled or crab-cracked shells. Many wading birds, racoons and opossums occur at the site but none were observed eating *Cerithidea*. MacDonald (1976) found that whole and fragmented shells of *C. californica* were not uncommon in shore bird droppings. He also recorded crab predation in this species and suggested that bottom fish that enter marsh creeks at high tides prey on *Cerithidea*.

The ecology of *C. (Cerithideopsis) californica* has been the subject of several papers (Race, 1982; Whitlatch and Obrebski, 1980; MacDonald, 1967, unpublished dissertation). This species differs from its other American congeners in having a geographic distribution in essentially temperate climates. It also displays a wide range of physiological tolerances. It can survive up to four hours' immersion in 40°C seawater and, in dry conditions, 65% of a population can survive exposure between 11–15 days (Race, 1982:345). Race (1982) studied the interaction between the endemic *C. californica* and its introduced Atlantic ecological equivalent, *Ilyanassa obsoleta* (Say, 1822) in San Francisco Bay. The latter species is an omnivore that preys on the eggs and young of *C. californica* which it has displaced in much of its former habitats. During the summer, *C. californica* attains densities of 1,000 snails per square meter. It appears to be immersed in water more often than *C. scalariformis.* Race (1982:342) found that during low tide, about two-thirds of the snails were on tidal creek bottoms and one-third out of the water. On cold days most were burrowed into mud on creek bottoms. My observations of *C. scalariformis* showed that it tends to remain out of water except during very high tides or when spawning. I did not find burrowing to be common, even during cold spells. MacDonald (1967) recorded predation on *C. californica* by shore birds and suspected that bottom fishes also preyed on them during high tides. Large individuals were eaten by the crab, *Pachygrapsus crassipes.*

SYSTEMATIC CONCLUSIONS

Genus *CERITHIDEA* Swainson

Cerithidea Swainson, 1840:198,203,342. Type-species: *Melania lineolata* Griffith and Pidgeon, 1934, *non Strombus lineolatus* Gray, 1828 (= *Cerithium obtusum* Lamarck, 1822), by subsequent designation of Pilsbry and Harbison, 1933.—Adams, A., 1854:292–293;—Tryon, 1882:251;—Fischer, 1887:682;—Cossmann, 1906:113;—Thiele, 1929:206–207;—Wenz, 1938:742;—Bequaert, 1942a:20;—1942b:1;—Olsson and Harbison, 1953:290–291;—Van Benthem Jutting, 1956:428–429;—MacNeil, 1960:39;—Ladd, 1972:39.

Phaenommia Mörch, 1860:80. Type-species: *Cerithidea Charbonieri* Petit (= *Cerithium charbonieri* Petit de la Saussaye, 1851), by monotypy.

Aphanistylus Fischer, 1884:682. Type-species: *Cerithidea Charbonniere* (sic) Petit (= *Cerithium charbonnieri* Petit de la Saussaye, 1851), by monotypy.

Diagnosis: Members of genus *Cerithidea* s.l., characterized by elongate, turreted shells of thin to moderate texture sculptured with spiral ridges and prominent axial ribs, sometimes with thick varices. Apeture large, oval with smooth outer lip and short anterior canal. Lower lip projects beyond columella base (Fig. 5, C). Radular ribbon short, all teeth have cusps, and shafts of maginal teeth have flaring, flattened process. Operculum thin, corneous, circular and multispiral with central nucleus. Animal with moderately long tentacles, eyes at their swollen bases. Mantle edge smooth, all species have pallial siphonal eye. Ctenidium reduced, filaments low and broad, osphradium narrow and ridge-like. Hypobranchial gland broad and extends from ctenidium over roof of pallial cavity to cover rectum. Pair of salivary glands passes through nerve ring and large swollen crop present posterior to nerve ring. Stomach has numerous sorting ridges and large gastric shield. Long style sac and style advance from stomach and terminate at pericardium. Females have ovipositor on right side of foot. Spermatophore bursa and sperm pouch lie in proximal outer lamina of pallial oviduct and seminal receptacle in proximal inner lamina. Males aphallate, sperm dimorphic. Spawn deposited in jelly strings which contain egg capsules. Development planktotrophic or lecithotrophic. Amphibious adults live in intertidal environments. Most species tend to avoid rising tide and undergo seasonal migrations.

Remarks: Thiele (1929:206) divided the genus *Cerithidea* Swainson, 1840 into two subgenera, *Cerithidea* s.s. and *Cerithideopsis*. He split the latter taxon into two sections, *Cerithideopsis* s.s. and *Cerithideopsilla*. Wenz (1938:742) considered the genus *Cerithidea* to comprise four subgenera, *Cerithidea* s.s., *Cerithideopsis, Cerithideopsilla* and, for a fossil species, *Cerithideops* Pilsbry and Harbison, 1933. According to Bequaert (1942a:20), his citation of *Cerithidea decollata* (Linnaeus, 1767), on the authority of Makiyama (1936), as the type-species of the genus is incorrect. *Cerithidea decollata* is credited to Bruguière (1838). *Cerithium obtusum* Lamarck, 1822 was desginated the type-species of *Cerithidea* by Pilsbry and Harbison (1933:115). Bequaert (1942a:20–21) has thoroughly reviewed the history of the selection of a type-species for this genus and may be consulted for more details. Shell characters, radular morphology and ecological differences appear to warrant Wenz's (1938) recognition of the three Recent subgenera within the genus. Neither Bequaert (1940:1) nor Van Benthem Jutting (1959:428) recognized the subgeneric taxa proposed by Thiele (1929), but included all species in *Cerithidea*. Retgeren Altena (1940), in his revision of some Indo-West-Pacific *Cerithidea* species, recognized the subgeneric status of *Cerithideopsilla* and assigned four living species to it. Following Thiele (1929), he later (1942:7) referred *Cerithideopsilla* to a "Section" under the subgenus *Cerithideopsis,* but gave no reason for this change of status.

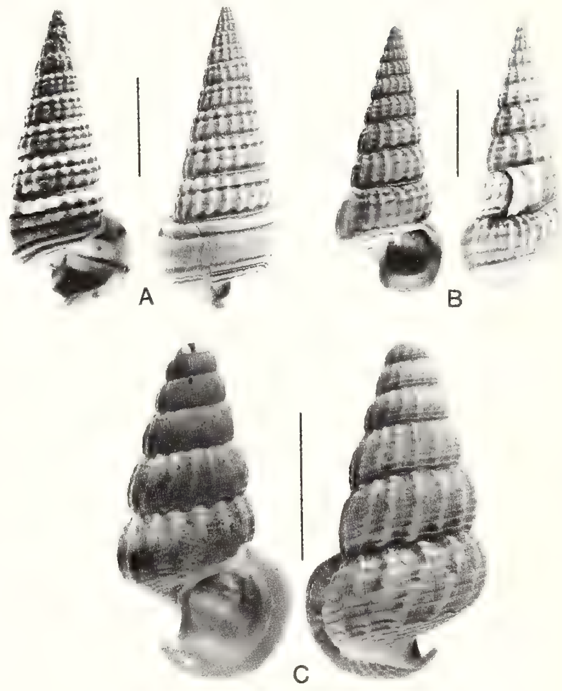

Fig. 5. Type-species of *Cerithidea* subgenera: **A)** *Cerithidea (Cerithideopsilla) cingulata* from Ras Tanura, Saudi Arabia (USNM 622154; 27.4 mm); **B)** *Cerithidea (Cerithideopsis) pliculosa* from El Zacatal, Campeche, Mexico (USNM 702909, 22.6 mm); **C)** *Cerithidea (Cerithidea) obtusa* from Kuala Selangor, Malaysia (USNM 778778, 39.7 mm).

The subgenus *Phaenommia* Mörch, 1860 was proposed to accommodate *Cerithidea charabonnieri* Petit de la Saussayse, 1851. The shell of this species does not seem to differ significantly from those of *Cerithidea* s.s. species and since nothing is known of the radula or soft parts of this species I am synonymizing it with *Cerithidea* s.s. pending further information.

Cerithidea largillierti Philippi, 1849, heretofore referred to *Cerithidea*, does not seem to fit the limits of any subgenera recognized in this study. I agree with Bishop (1979:77), who suggested that it might better be referred to a new genus. More material and anatomical work on this uncommon species are needed before a sound taxonomic decision is reached.

According to Cossmann (1906:113–114), the genus *Cerithidea* occurs as far back in the fossil record as the Maastrichtian of the Cretaceous. Members of this group are common in the Eocene of the Paris Basin indicating that they were abundant in the Tethys Sea.

Three Recent subgenera are herein recognized: *Cerithidea* s.s., *Cerithideopsilla*, and *Cerithideopsis*. The type-species of each of these taxa are depicted in Figure 5.

C. (Cerithidea) Swainson, 1840 [Type-species: *Cerithidea obtusa* (Lamarck, 1822), by s.d.]

Diagnosis: Species characterized by thin textured shells, some markedly decollate, having prominent axial ribs with or without spiral sulci, wide mouthed apertures, smooth rounded outer lips and rudimentary anterior canals (Fig. 5, C). Ctenidium rudimentary. Network of blood vessels in mantle roof functions like pulmonate lung (Pelseneer, 1895). Osphradium either lacking (Pelseneer, 1896) or much reduced. Rachidian tooth of radula narrow with small central cusp. Outer marginal tooth lacks cusps and has wide flange on outer side of basal shaft.

Remarks: Cerithidea s.s. species tend to live on mangroves well above the tide mark and have an Indo-West-Pacific distribution. They are frequently found attached to leaves and branches by glutinous threads. Development may be planktotrophic or lecithotrophic. Although Cossmann (1906:113–114) traced this genus back to the Maastrichtian of the Cretaceous and described many species from the Eocene of the Paris Basin, it is unlikely that these forms are the same as Recent *Cerithidea* s.s. Ladd (1972:27) recorded fossils of *Cerithidea obtusa* from the Miocene of Saipan. Figures of his samples do not look like the living species but are undoubtedly referred to *Cerithidea* s.s. MacNeil (1960:39) recorded fossil *Cerithidea rhizophorarum* A. Adams, 1854 from the Pleistocene of Okinawa and Regteren Altena (1942) cited it from the Pliocene of Java. It would thus appear that *Cerithidea* s.s. dates at least as far back as the Pliocene.

C. (Cerithdeopsilla) Thiele, 1929 [Type-species: *Cerithidea fluviatilis* (Potiez and Michaud, 1838); = *Cerithidea cingulata* (Gmelin, 1790), by o.d.];—Regteren Altena, 1942:212.

Diagnosis: Species distinguished by shells sculptured with axial ribs crossed by spiral grooves and generally divided into three spiral rows of tubercles. Posterior extension of angular outer lip forms flaring, wing-like process extending nearly halfway up penultimate whorl. Anterior extension of outer lip partially crosses over narrow, deeply notched, anterior canal. Aperture narrow, oval and peristome in adults continuous (Fig. 5, A). Rachidian tooth of radula wide, rounded and convex at top, pentagonal, and has small, equal sized cusps. Base broad, bearing long, wide glabrella. Lateral tooth has long twisted lateral extension while outer marginal tooth has numerous small cusps and lacks wide basal flange seen in *Cerithidea* s.s.

Remarks: Species have an Indo-Pacific distribution and live on intertidal, muddy, sandy estuarine flats, frequently near mangroves and sometimes on their roots. The type-species of the subgenus undergoes planktotrophic development. This subgenus is recorded from the Miocene of the Philippines, India, Japan, and Taiwan and has also been cited from the Pliocene of the Philippines, Java, Sumatra, and Japan (Regteren Altena, 1942). Although some of these identifications may be wrong, *Cerithideopsilla* may be reasonably traced back to the Miocene and appears to be the earliest subgenus found in the fossil record.

C. (Cerithideopsis) Thiele, 1929 [type-species: *Cerithidea iostoma* (Pfeiffer, 1839); = *Cerithidea pliculosa* (Menke, 1892), by o.d.].

Diagnosis: Shell moderately decollate, characterized by thickened varices and straight columella. Short, wide anterior canal, thick outer lip. Axial sulpture dominant with few spiral grooves and cords (Fig. 5, B). Rachidian tooth of radula broad, pentagonal, and has concave top and long, central cusp flanked by two denticles on each side. Base of tooth wide bearing long glabrella. Lateral tooth has long, twisted, lateral extension. Outer marginal tooth bears numerous small cusps and has wide flange on basal shaft.

Remarks: Species are amphibious and restricted to New World estuaries where they live on sandy, muddy flats in salt marshes and mangroves, on *Spartina* and *Juncus* grasses and on *Salicornia* bushes at the high intertidal zone. Some species live in the temperate zone and all species examined have lecithotrophic development. The Western Atlantic species of this group were monographed by Bequaert (1924b). *Cerithideopsis* is known from the Pliocene of Florida (Olsson and Harbison, 1953:291).

PHYLOGENY: Cladistic analysis of 19 characters comprising 38 character states (Table 5) derived from shell morphology, anatomy and patterns of radular dentition distributed among four taxa provided the cladogram shown in Figure 6. Six cladograms, derived from a reshuffling of taxa, showed identical trees. Each was derived with a total of 21 character changes among the 19 characters. Of these 21 changes, two (5 and 6) are reversals. The outgroup (ancestor) used was *Batillaria,* subfamily Batillariinae. It would

Table 5. Comparison of three subgenera of *Cerithidea* using 19 characters and 38 character states (outgroup is *Batillaria*).

	Taxa			
Character	*Cerithidea*	*Cerithideopsis*	*Cerithideopsilla*	Outgroup
SHELL				
1. shell thickness				
strong (0)				
thin (1)	1	1	0	0
2. decollation				
absent (0)				
present (1)	1	0	0	0
3. spiral sculpture				
weak (1)				
strong (0)	1	1	0	0
4. outer lip extension				
absent (0)				
present (1)	0	1	1	0
5. outer lip				
thickened (1)				
not thickened (0)	1	1	0	0
6. prominent varices				
absent (1)				
present (0)	1	0	1	0
7. anal canal				
absent (1)				
present (0)	1	1	0	0
8. anterior canal				
wide (1)				
narrow (0)	0	1	0	0
9. peristome				
rounded (0)				
not rounded (1)	0	0	1	0
ANIMAL				
10. ctenidium				
rudimentary (0)				
developed (1)	1	0	0	0
11. osphradium				
reduced (1)				
not reduced (0)	1	0	0	0
12. pallial eye				
present (1)				
absent (0)	1	1	1	0
13. crystalline style				
long (1)				
short (0)	1	1	1	0
RADULA				
14. rachidian narrow with single cusp (1); with many cusps (0)	1	0	0	0
15. rachidian with long basal plate (1); without long basal plate (0)	1	0	0	0
16. rachidian with cusps on basal plate (0); without cusps on basal plate (1)	1	1	1	0
17. lateral tooth with long twisted extension (0); without extension (1)	0	0	1	0
18. outer marginal with broad basal flange (0); without flange (1)	0	0	1	0
19. outer marginal with many cusps (0); without many cusps (1)	1	0	0	0

have been better to have used a closer sister group in the subfamily Potamidinae but no comparable anatomical and radular studies of species within this group exist.

Polarities of shell characters (characters 1–9) are either difficult to determine or suspect because of possible parallelisms and reversals. As Davis (1979:34) noted, convergence is an underestimated phenomenon in the evolution of shell morphology. Accordingly, the polarities determined for this set of shell characters are based mainly on outgroup comparison (see Table 5). Other evidence for determining polarity and a discussion of some of these characters are given below:

Character 1. A strong heavy shell is usually associated with the larger, more highly sculptured species, especially some of the fossil ones in the Potamidinae. A thinner, decollate shell is better adapted to tree climbing and is probably a derived trait brought about by radiation into the supratidal mangrove habitat where fish and crab predation are not as important.

Character 2. Marked decollation is known only among the tree dwelling *Cerithidea* s.s., and is not common among other potamidids. A minor degree of decollation exists in *Cerithideopsis* species, but this is frequently due to severe erosion of the earlier whorls. Consequently, the decollate condition appears to be a derived character.

Few anatomical characters were used because of the lack of information about comparable structures and tracts in all of the taxa, especially in *Cerithideopsilla*. This is particularly true of the pallial gonoducts. Comments on anatomical characters follow:

Characters 10, 11. A well developed ctenidium and osphradium occur in nearly all potamidid species. Their rudimentary condition in *Cerithidea* s.s. is considered a derived feature that is probably due to their unusual tree dwelling habit.

Character 12. With the exceptions of *Tympanotonus* and *Pyrazus ebininus*, a pallial eye is not found in other potamidid genera and the presence of this structure in all *Cerithidea* species is surely a derived condition. The pallial eyes of the other taxa are probably not homologous with those of *Cerithidea* and are here attributed to convergence.

Character 13. A short crystalline style is found in *Batillaria* (Driscoll, 1972) and probably in other members of the Batillariinae, but it is a prominent feature of *Cerithidea*.

Polarities of radular characters were established by outgroup comparison. There have probably been parallelisms and reversals in the evolution of radular dentition because these structures seem to be closely correlated with the types of food eaten; therefore, they may not be reliable characters for establishing polarities. The characters and states are listed under characters 14, 15, and 19 (Table 5) may reflect a change of diet due to life in the mangroves.

Not enough is presently known of the developmental biology of *Cerithidea* species to make any meaningful systematic comparisons. A summary of available information appears in Table 4. Both planktotrophic and lecithotrophic development are known in *Cerithidea* s.s. and *Cerithideopsilla*. As mentioned earlier, it appears that widely dispersed, intertidal species tend to have planktotrophic larvae, but it is not now possible to suggest polarity of developmental types.

As regards ecology, *Cerithidea* s.s species have moved into the mangroves, well above the high tide mark and are obviously derived from ancestors who lived in the water. They are essentially a tropical group. The New World *Cerithideopsis* group live mainly at the high tide mark and some species are adapted for life in the semitropical or temperate zones. The Potamididae evolved in tropical seas and movement into temperate zones is probably a new development.

Using the characters discussed above, a hypothesis of the relationships among *Cerithidea* species is presented in Figure 6. According to this cladogram, the taxa *Cerithidea* and *Cerithideopsis* are more removed from the outgroup and share more synapomorphies with each other than with *Cerithideopsilla*. This last taxon, therefore, could be ranked differently than the other two. *Cerithideopsilla* has the most generalized characters and, in this respect, is regarded as the more primitive group. This subgenus also has the longest known fossil record, extending back to the Miocene (Regteren Altena, 1942). *Cerithideopsilla* species tend to live on muddy, sandy substrata as do *Batillaria* species. A direct conversion of the cladogram shown in Figure 6 to a classification that reflects the true phylogeny of this group is unwise. It is obvious that criteria for determining polarity in the transformation series of characters used in this analysis are weak and in many cases established solely on the basis of presence in the outgroup. We know too little of other potamidid groups to make comparisons that will provide clues about polarity. Moreover, the potential for convergence within the Potamididae and specifically in *Cerithidea* is, in my opinion, high. For example, many shell characters such as those seen in the aperture and lip are undoubtedly related to habitat, and supratidal species living in trees will have different shells than those confined to mud flats. It is also probable that more than one clade has radiated into a tree-climbing mode of existence with subsequent return of some species to

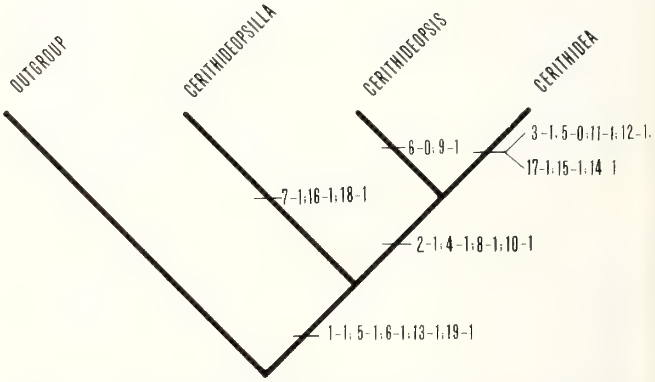

Fig. 6. A hypothesis of the relationships among *Cerithidea* subgenera based on a cladistic analysis of characters. Hyphonated numbers refer to characters and changes in character states, respectively.

the muddy substrate. Accordingly, I give the three taxa equal rank as subgenera of *Cerithidea*. Thus the classification given above should be used with caution and will undoubtedly change as more is known about the anatomy of other higher taxa. It would have been better to have a member of the subfamily Potamidinae as an outgroup, but no comparable anatomical study has been done on members of this group that would serve this purpose. An exception is *Tympanotonus,* but that study concerned the pallial gonoducts.

A survey of fossil and Recent potamidids shows an overall tendency within the Potamididae toward reduction of the expanded, sinuated outer lip, which in many fossil groups and some Recent ones is elaborate and variously produced. Indeed, many extinct higher taxa comprise species with elaborate outer lip morphology, and strong, highly sculptured shells such as seen in *Potamides* and *Pyrazus* species. The Batillariinae are more cerithiid-like in shell morphology than are the Potamidinae and exemplify the familial evolutionary trend to become more "streamlined." In this respect, *Cerithideopsilla* is indeed a more "primitive" *Cerithidea* taxon, having a pronounced expansion and sinus on the posterior outer lip adjacent to the anal canal.

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SHELL REDUCTION AND LOSS IN FISSURELLIDS: A REVIEW OF GENERA AND SPECIES IN THE *FISSURELLIDEA* GROUP

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ABSTRACT

Six species in three related genera, the *Fissurellidea* group, have a hypertrophied development of the mantle covering the head and foot, a broad rachidian tooth, and the shell vestigial or lacking.

Fissurellidea Orbigny, 1841, has a radially striate shell and comprises the type species *F. megatrema* Orbigny, 1841, in southern Argentina, *F. patagonica* (Strebel, 1907) in southern Chile and southern Argentina, and *F. bimaculata* Dall, 1871, in the northeastern Pacific. *Megatebennus* Pilsbry, 1890, proposed originally for the latter, is synonymized with *Fissurellidea*.

Pupillaea Sowerby, 1835, differs from *Fissurellidea* in having a higher shell profile and in having two shell layers offset at the margin. It comprises the type species *P. aperta* (Sowerby, 1825) in South Africa, and *P. annulus* (Odhner, 1932) in southern Chile. The latter has a ringlike shell, an extreme vestige.

Buchanania onchidioides Lesson, 1830, from southern Chile, here reported for the first time since its description, lacks a shell as an adult, but is otherwise like other members of the *Fissurellidea* group; it has a groove in which there is probably a shell in early stages. This genus completes the trend toward shell reduction in the tribe Fissurellidini.

Although shell reduction and loss is a prominent trend in opisthobranch and pulmonate gastropods, it occurs very infrequently in prosobranchs. Heretofore, a complete loss of shell has been known in prosobranchs only in the neritacean family Titiscaniidae.

In the Fissurellidae, a trend toward shell reduction and loss is evident in three genera here called the *Fissurellidea* group. These genera—*Fissurellidea* Orbigny, 1841, *Pupillaea* Sowerby, 1835, and *Buchanania* Lesson, 1830—differ from most other large-bodied fissurellids in having a thick, leathery mantle enveloping the head and foot. Species of *Fissurellidea* have a highly reduced, vestigial shell; one species of *Pupillaea* has an even more reduced shell; and the complete loss of the shell in the adult stage of *Buchanania* Lesson, 1830, is first reported here.

The taxonomy of genera and species comprising this group has been confused in the literature. All three genera are represented in the Magellanic faunal province, which encompasses southern Chile and southern Argentina. Field work in Chile in 1975, and in Argentina in 1978, enabled me to collect four of the relevant species and to resolve a number of pertinent problems. Here the genera are newly defined and the species, totaling six, are briefly treated, basing the classification on characters of shell morphology and external anatomy.

Abbreviations for museums mentioned in the text are: AMNH, American Museum of Natural History, New York; LACM, Los Angeles County Museum of Natural History; MACN, Museu Argentino de Ciencias Naturales, Buenos Aires; NM, Natal Museum, Pietermaritzburg, South Africa; USNM, United States National Museum of Natural History, Washington, D.C.

In the descriptions that follow, the specimens mentioned were collected in the lower intertidal zone unless otherwise indicated. Measurements of shells and bodies are given in this order: length, width, and height. Latitude and longitude are given for localities in southern Chile and Argentina, where there are many islands, but latitude only is given where the coastlines are continuous. Except where noted, specimens of shells and bodies are illustrated with the anterior to the top.

Family FISSURELLIDAE
Subfamily EMARGINULINAE

I follow the classification of Thiele (1929) in recognizing two subfamilies in the Fissurellidae: the Emarginulinae and Fissurellinae, basing the division upon a major distinction in radular characters.

The subfamily Emarginulinae, which appeared in the Mesozoic, has a rachidian of varying breadth and the massive outer lateral tooth is bicuspid. In constrast, the Cenozoic appearing Fissurellinae have a rachidian tooth narrow and

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tapered at the tip and an outer lateral tooth with four cusps (except three in *Macrochisma* Sowerby, 1839).

I subdivide the Emarginulinae into tribes, as further treated in other work in progress.

Tribe FISSURELLIDINI Pilsbry, 1890

[*ex* Fissurellidinae]

DIAGNOSIS. Shell (if present) relatively low; apex resorbed in mature shells; foramen at summit, relatively large, bordered by discrete callus ring on interior surface; callus not truncate nor depressed posteriorly. Animal much larger than shell, not retractable within it. Muscle scar reduced, lacking inwardly directed hook-shaped process. Rachidian tooth of radula ranging from extremely broad to narrow; outer lateral teeth bicuspid.

INCLUDED GENERA. *Lucapinella* Pilsbry, 1890; *Leurolepas* McLean, 1970; *Fissurellidea* Orbigny, 1841; *Pupillaea* Sowerby, 1835; *Buchanania* Lesson, 1830.

Genera differ from those of the Diodorini, some genera of which also have large-bodied animals, in lacking, on the shell interior, a depression posterior to the callus ring that surrounds the foramen, and in lacking the hook-shaped process of the shell muscle that characterizes all other members of the Emarginulinae.

Lucapinella, which is not treated further here, has a relatively large shell compared to the size of the animal, and the head and foot are not fully covered by the mantle. The mantle of *Leurolepas* fully envelops the head and foot as in the *Fissurellidea* group of genera, but the rachidian is relatively narrow and the inner laterals are nearly equal in size to the rachidian. Earlier (McLean, 1970), I considered the monotypic *Leurolepas* to be a member of the Fissurellinae, but here assign it to the Fissurellidini because the enlarged outer laterals are bicuspid like those of other Emarginulinae.

EXCLUDED GENERA. Pilsbry (1890) intended the Fissurellidini (which he proposed at the subfamily level) to include *Megathura* Pilsbry, 1890, which also envelops the head and foot, though the shell remains relatively large. *Megathura* is here allocated to the tribe Diodorini because the muscle retains the inwardly directed hook-shaped process, a character not considered by Pilsbry. Such other large-bodied genera as *Cosmetalepas* Iredale, 1924, and *Monodilepas* Finley, 1927, do not envelop the head and foot; they also have the hook-shaped process to the muscle and are referred to the Diodorini. *Amblychilepas* Pilsbry, 1890, has quadricuspid outer laterals and is allocated to the Fissurellinae.

The *Fissurellidea* Group of Genera

GENERIC DISTINCTIONS. Genera are defined on shell characters: sculptured with radial striae in *Fissurellidea*, with sharply differentiated margin in *Pupillaea*, and the shell lost altogether in mature *Buchanania*.

SHELL CHARACTERS. The shell (where present) is saddle-shaped, with ends raised; sculpture consists of broad radial ribs; on the interior, the callus ring surrounding the foramen is narrow and there is a narrow raised border along the shell margin. The foramen is proportionately larger than in most other fissurellid genera.

Shells comparable to the size of the animal are known in small specimens, those with shell lengths about ¼ the length of large shells. With growth the size of the animals increases faster than the shell. The expansion of the foramen also increases at a proportionately faster rate than growth of the shell.

Juvenile shells of *F. bimaculata* resemble those of *Diodora*, still retaining the apical whorl posterior to the foramen at a length of 2.5 mm. Postlarval shells have not been identified, but are probably like those of *Diodora*, in which the foramen appears on the anterior slope of the shell and for a very brief period leaves a selenizone behind, as illustrated by McLean (1984, figs. 7C, 7D).

ANATOMY. Odhner (1932) compared internal anatomy in some of the species treated here (see the citations in the synonymies) and Rodrigo-Trigo (1930) detailed the anatomy of *Fissurellidea megatrema*. Ghiselin, et al. (1975) reported that "*Megatebennus*" *bimaculatus* and some other fissurellids have a crystalline style.

The hypertrophy of the mantle in the *Fissurellidea* group is a modification of the characteristic mantle edge of fissurellids. Stasek and McWilliams (1973) showed that the fissurellid mantle edge has three discrete folds: 1) the outer fold, which secretes and maintains contact with the shell edge, 2) the middle fold, which extends up above the shell edge and may envelop the shell without obliterating the sculpture, and 3) the inner fold, which extends down to envelop the foot and frequently the head of the animal.

In the *Fissurellidea* group, there is a strong development of the middle fold covering the shell and, a massive development of the inner fold that extends over the head and foot. The hypertrophied development of both folds causes the shell to be essentially internal. For the greater part of its length the mantle roof above the gills consists of the thickened middle fold with no shell support.

Exterior coloration varies in all species. Colors include yellow, orange, brown, gray, or black, often with radiating patterns of lighter mottling. Mantle color is unrelated to shell color. The living animals have the general appearance of large-bodied dorid nudibranchs.

Small or half-grown specimens of *Fissurellidea* may partially or completely retract the thin shell-enveloping middle fold, thereby exposing the shell. Preserved specimens of the same species may exhibit varying amounts of middle fold retraction [compare Figures 15 and 16]. When shells are removed from preserved specimens of *Fissurellidea* by cutting back the middle fold, the small, shell-secreting outer fold may be observed within the groove that marks the position of the shell.

The snout (Figs. 21, 33) is often concealed between the foot and the inner fold of the mantle in preserved specimens.

RADULAR CHARACTERS. The radula of the *Fissurellidea* group is not unlike that of *Diodora* and other members of the tribe Diodorini. The rhomboid-shaped rachidian tooth characteristic of emarginuline fissurellids has its broadest expression in this tribe. In the adults of some species the rachidian may be three times as broad as high. However, the morphology of the central field (rachidian and inner laterals) in all fissurellids is not especially important because these teeth lack strong cutting edges. The major functioning teeth are the large, bicuspid outer laterals, sometimes called the "dominant" teeth. Expansion of the broad rachidian provides the means by which the necessary separation between the opposing dominant teeth can be achieved. Hickman (1981) showed that the strong asymmetry of the radular ribbon of all fissurellids is caused primarily by the need for opposing dominants to fold together, zipper fashion, when the radula is not in its feeding stroke.

Barnard (1963) noted that the breadth of the rachidian tooth increases with growth in *Pupillaea aperta*. Such changes with growth are also true of the *Fissurellidea* species. Hence, the relative breadth of the rachidian does not provide a reliable taxonomic character at the specific level.

HABITAT. All species of the *Fissurellidea* group occur on rocky bottoms in the low intertidal and sublittoral zones. They occur on undersides of rocks or beneath projecting ledges where there is a thick growth of such encrusting organisms as sponges and compound ascidians. None of the species can strongly adhere to the rock substratum; all may easily be detached when the animals are exposed at low tide.

Ghiselin et al. (1975) reported that the gut of *"Megatebennus" bimaculatus* contained sponge spicules and that specimens in laboratory aquaria fed upon compound ascidians. Miller (1968) showed that *Lucapinella callomarginata* (Dall, 1871) feeds on sponges.

DISTRIBUTION. The center of distribution for the *Fissurellidea* group is the Magellanic faunal province. Two of the three species of *Fissurellidea* occur there and the third occurs in the northeastern Pacific. *Pupillaea* has one species in the Magellanic province and another in South Africa. *Buchanania* has one species in the Magellanic province.

FOSSIL RECORD: Wenz (1938), followed by Keen (1960), indicated a European Eocene record for *Fissurellidea*. I have traced the record to *Fissurella minosti* Melleville, 1843, placed in *Fissurellidea* by Cossmann and Pissarro (1910–1913, pl. 2, fig. 7). However, I assign that species to the tribe Diodorini because the interior view given by Cossmann and Pissaro shows that the foramen is circular and the interior callus is truncate posteriorly. For the same reason, I also reject Wenz's Eocene subgenus *Profissurellidea* as a member of the tribe.

Wenz (1938) erroneously reported a few ("wenige") species of *Pupillaea* in the Pliocene of "South America." I have traced the record to *"Pupillia aperta tehuelcha"* Ihering, 1907, which is here treated in the synonymy of *F. megatrema*.

Genus *FISSURELLIDEA* Orbigny, 1841

Fissurellidea Orbigny, 1841: 447. Type species (monotypy): *F. megatrema* Orbigny, 1841.

Megatebennus Pilsbry, 1890: 182. Type species (original designation): *Fissurellidea bimaculata* Dall, 1871.

SHELL. Small relative to size of animal, low, ovate-rectangular; ends raised relative to sides. Sculpture of broad, low ribs separated by narrow grooves. Foramen oval, very large; interior callus ring narrow. Muscle scar very narrow, close to shell margin; shell margin finely crenulated by radial sculpture, interior of margin with rounded, slightly projecting border. Color buff, with pattern of darker rays.

In gerontic specimens, growth may stop and the shell edge may become either thinner or thicker, or upwardly deflected. Such changes in the shell should have no important effect because the shells have little functional significance.

MANTLE. Length of body 3 to 7 times shell length; mantle lobes thickened, enveloping shell and extending down to cover head and foot.

RADULA. The breadth of the rachidian varies among the species from nearly equal to the height, to almost three times the height, but as discussed above, this serves only to keep the massive outer lateral teeth well separated.

REMARKS. Shells of *Fissurellidea* are flatter and do not have the offset margin of *Pupillaea*.

Species of *Fissurellidea* are: *F. megatrema* Orbigny, 1841, southern Brazil to southern Argentina; *F. patagonica* (Strebel, 1907), southern Argentina to southern Chile; and *F. bimaculata* Dall, 1871, northeastern Pacific. Distributions of the three species are shown in Figure 1.

SYNONYMY. *Megatebennus* Pilsbry, 1890, is here synonymized with *Fissurellidea*. Until now *Megatebennus* was used for its type species, *F. bimaculatus*, in the northeastern Pacific, and the Magellanic *F. patagonicus*. Pilsbry (1890:182) stated that *Megatebennus* differed from *Fissurellidea* "in the much greater proportional size of the shell, more elevated body, the foot (viewed ventrally) almost as extensive as the mantle, the margin of the latter not at all thickened, and the shell not white-bordered above." However, Pilsbry's knowledge of the type species of *Fissurellidea* was based on misleading accounts in the literature. The white-bordered appearance to the shell of *F. megatrema* in Orbigny's original illustration, which was regarded as significant by Pilsbry, is a possible gerontic expression, not a character of generic importance. Orbigny's figure of the animal of *F. megatrema* is also misleading in showing a flattened body. The proportional size distinctions claimed by Pilsbry are not sustained here. None of Pilsbry's comparisons serve to separate *F. bimaculata* from the two species occurring in South America.

The radula of *Fissurellidea bimaculata* has a rachidian tooth not as broad as that of the other two species, but this does not suffice for generic separation, considering how this character varies among species in other fissurellid genera.

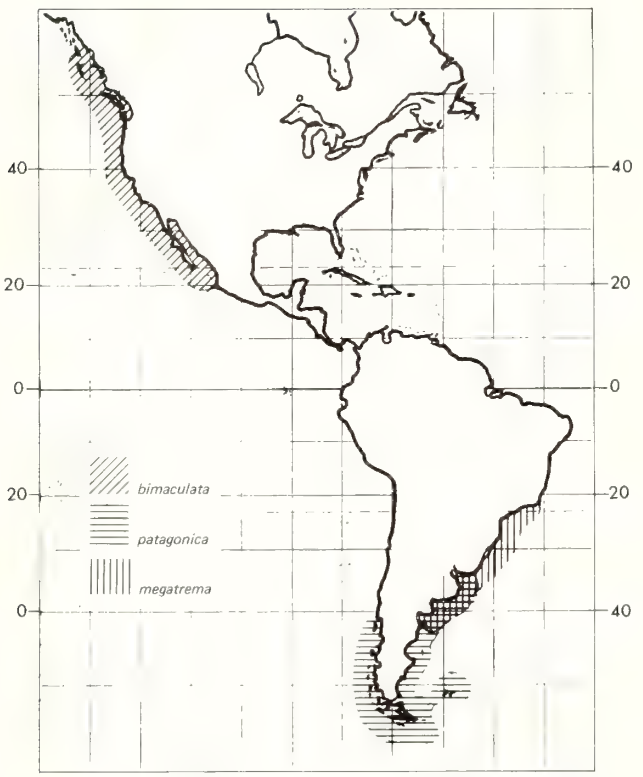


Fig. 1. Distribution of *Fissurellidea* species in North and South America.

Fissurellidea megatrema **Orbigny, 1841**
Figures 2–9

Fissurellidea megatrema Orbigny, 1841: 477, pl. 63, figs. 5–10; Rodrigo-Trigo, 1930: 281 [anatomy].

"Fissurellidea hiantula," of authors: Pilsbry, 1890: 179–180, pl. 43, figs. 89–93 [copy Orbigny's figs. of *F. megatrema*]; Ihering, 1927: 103; Odhner, 1932: 294, figs. 26, 27 [anatomy], fig. 41.3 [radula], pl. 5, figs. 9–11 [shell]; Carcelles, 1944: 240, figs. 3–7; Carcelles, 1950: 50; Carcelles and Williamson, 1951: 253; Barratini and Ureta, 1960: 92, Castellanos, 1970: 17, pl. 1, fig. 6; Rios, 1975: 17, pl. 3, fig. 32; Figueiras and Sicardi, 1980: 180. Not *Fissurella hiantula* Lamarck, 1822, v. 6(2): 14.

Pupillia aperta tehuelcha Ihering, 1907: 399.

SHELL. Oval, thin; anterior slope slightly concave, elevating front margin. Sculpture of broad radial ribs, separated by incised grooves, concentric sculpture of growth increments, faintly rayed in gray or brown. Foramen elongate-oval, broader posteriorly, at least ⅓ shell length in large shells, proportionately less in smaller shells. Margin finely crenulate at edge, interior with rounded, projecting border; margin of gerontic specimens often upturned, some appearing white-bordered on upper surface due to cessation of pigmentation at shell edge.

Dimensions of large shell: 27.4 × 19.4 × 5.7 mm (LACM 34932, Mar del Plata, Argentina).

MANTLE. Shell positioned at anterior third, body up to seven times length of shell; mantle surface thickened, usually with radiating rows of large swellings; overall color yellow, gray, or brown, with lighter colored large swellings, usually with dark pigmentation in fine reticulate pattern and scattered, irregular black markings midway on sides; some specimens gray or yellow overall with no apparent indication of large swellings.

Dimensions of largest preserved specimen: 71 × 45 × 25 (LACM 34935, Mar del Plata, Argentina).

Preserved specimens usually have the middle fold of the mantle partially retracted, exposing a small area of the shell surface.

RADULA. Rachidian tooth broad, 2 to 3 times as broad as high (Fig. 5).

DISTRIBUTION AND OCCURRENCE. Rio de Janeiro, Brazil (22°53′ S) (Rios, 1975), south to Punta Ninfas, Chubut Province, Argentina (43°21′ S) (LACM). Occurring offshore in Brazil and Uruguay. At Mar del Plata, Argentina, and to the south, also occurring in the intertidal zone on undersides of rocks and overhanging ledges.

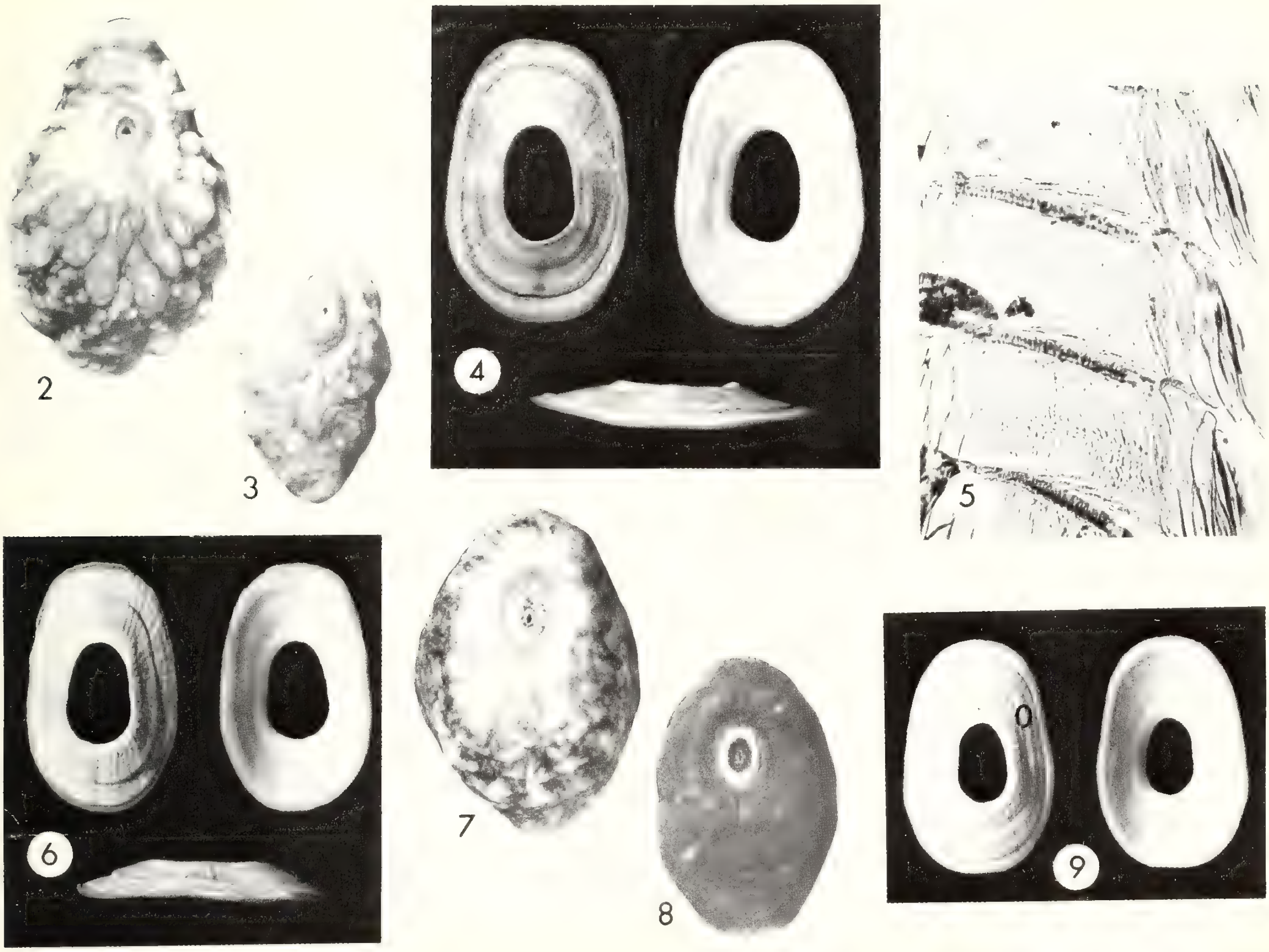
TYPE MATERIAL AND LOCALITY. I examined two syntypes of *Fissurellidea megatrema* in the Paris Museum in August 1980. Type locality: Ensenada de Ros, [15 "leagues" S of] Río Negro, Argentina [approximately 41° S].

MATERIAL. LACM, 20 lots, intertidal zone, from numerous localities in the vicinity of Mar del Plata, Buenos Aires Province, Argentina, collected by C. J. Risso-Dominguez, 1964–1973. LACM, 2 lots, intertidal and dredged offshore, Golfo Nuevo, Chubut Province, Argentina, collected by J. H. McLean on R/V HERO, July 1978. LACM, 45–55 m, S of Punta Ninfas, Chubut Province, Argentina, J. H. McLean on R/V HERO, July 1978.

COMPARISONS. The mature shell of *Fissurellidea megatrema* (Fig. 4) is broader and more oval than that of the other two species and the foramen is larger and broader posteriorly, and proportionately the largest among the three species. The radiating rows of swellings in the mantle surface are characteristic, not shared by the other species, though *F. bimaculata* has small tubercles in a similar radiating pattern.

SYNONYMY. Orbigny's illustration of *F. megatrema,* which were copied by Pilsbry (1890), show the mantle with a smooth gray surface and a shell with a white border. As mentioned above, the white bordered appearance of the type figure is not considered a generic or even specific character. The foramen in the original illustration is sufficiently large to dispel any possibility that it was based on the species identified here as *F. patagonica.* The shell figured by Orbigny is clearly conspecific with those illustrated here as *F. megatrema.*

Orbigny's figure of the animal does not show radiating rows of large swellings nor the pattern of scattered clumps of



Figs. 2–9. *Fissurellidea megatrema.* **Fig. 2.** Preserved specimen with shell intact, relaxed at fixation. Cabo Corrientes, Mar del Plata, Buenos Aires Province, Argentina (38°01′ S), C. J. Risso-Dominguez, February 1972. LACM 34935, 72 × 46.5 × 26 mm. **Fig. 3.** Small preserved specimen with shell intact. Punta Gruta, Mar del Plata, Argentina (38°00.5′ S), C. J. Risso-Dominguez, 11 April 1971. LACM 34934, 23 × 15 × 8 mm. **Fig. 4.** Shell. 55 m, Mar del Plata, Argentina (approximately 38°00′ S), A. Pinto, 1962. AMNH 147740, 27.8 × 18.1 × 4.0 mm. **Fig. 5.** Radular ribbon, light microscope preparation. Cabo Corrientes, Mar del Plata, Argentina (38°01′ S), C. J. Risso-Dominguez, February 1972. LACM 34936, horizontal width of field 0.8 mm, length of preserved specimen 44 mm, shell length 14.8 mm. **Fig. 6.** Shell. 45–55 m, S of Punta Ninfas, Chubut Province, Argentina (43°15–21′ S), J. H. McLean, 17 July 1978. LACM 78–86, 17.7 × 10.9 × 3.1 mm. **Fig. 7.** Preserved specimen with shell intact. 20–50 m, between Punta Ninfas and Punta Cracker, Golfo Nuevo, Argentina (42°54′ S), J. H. McLean, 18 July, 1978.LACM 78–89, 61 × 42 × 29 mm. **Fig. 8.** Preserved specimen with shell intact. Same locality as Fig. 7. LACM 78–89, 45 × 29 × 21 mm. **Fig. 9.** Shell. Same localitay as Fig. 6. LACM 78–86, 16.3 × 10.6 × 3.2 mm.

dark pigmentation characteristic of most specimens of this species. This would raise a serious question about the identity of Orbigny's material were it not for the fact that some freshly collected specimens do not show the usual pattern. Two specimens from the same haul in the Golfo Nuevo are shown in Figures 7 and 8. The specimen in Figure 8 is gray and has barely a trace of the swellings; the specimen in Figure 7 clearly shows the swellings. This demonstrates that the specimen illustrated by Orbigny is within the possible range of variation in this species.

Most previous authors have used the older name *Fissurella hiantula* Lamarck, 1822, for this species. That assignment dates from Pilsbry (1890: 179), who stated: "This is unquestionably the true *hiantula* of Lamarck, agreeing with his description, and with the figure in Born's Test. Mus. Caes. Vindob., p. 414, vignette fig. F." No matter what the identity of the figure in Born (1778), which is further discussed below, Lamarck's reference to this figure must be discounted, because Mermod (1950: 708, fig. 18) located type material of *F. hiantula* in the Lamarckian collection. Mermod illustrated three specimens, none of which have foramina sufficiently large to be conspecific with *Fissurellidae megatrema*. Mermod considered Lamarck's specimens to have come from South Africa; Kilburn and Rippey (1982: 35) have used the name in the combination *Amblychilepas scutellum hiantula* (Lamarck, 1822), for a South African species.

I have examined the vignette figure in Born (1778: 414) and am certain that it is based on the species here treated as *Pupillaea aperta*. The shell depicted has dark rays and a sharply defined white border; the foramen is not broader posteriorly, as expected in *F. megatrema*. Pilsbry's mistaken conviction that this figure represented the Argentinean species must have been the corroborating point that misled him to propose *Megatebennus*, for which the major justification was the supposed lack of the white border.

"Pupillia aperta tehuelcha" Ihering was based on an unillustrated Pliocene specimen from the Araucanian Formation at Sierra Laziar, Argentina. Ihering used the generic and specific combination because he incorrectly considered *F. megatrema* a synonym of the South African *Pupillaea aperta*. The only difference from the living Argentinian species, with which he compared it, was that the radial sculpture was slightly stronger ("un peu plus forte"). In the absence of an illustration, the name is retained in the synonymy of *F. megatrema*, in keeping with Ihering's intentions.

***Fissurellidea patagonica* (Strebel, 1907)**

Figures 10–18

Megatebennus patagonicus Strebel, 1907: 98, pl. 2, figs. 23a–f; Strebel, 1908: 79; Melvill and Standen, 1914: 116; Odhner, 1932: 294, figs. 22–25 [anatomy], fig. 41.4 [radula], pl. 5, figs. 4, 5 [whole animal]; Riveros-Zuñiga, 1951: 133, fig. 37; Powell, 1951: 85; Carcelles, 1950: 50, pl. 1, fig. 8; Carcelles and Williamson, 1951: 253; Dell, 1971: 193; Figueiras and Sicardi, 1980: 180.

SHELL. Elongate-oval, thin to moderately thick. Sculpture of broad radial ribs, separated by incised grooves; concentric sculpture of growth increments, shells faintly rayed in gray or brown. Anterior and posterior ends slightly raised. Foramen elongate-oval, ¼ to ⅓ length of shell. Margin finely crenulate at edge, interior with rounded, projecting border; gerontic specimens may have thinner shells at margin.

Dimensions of large shell: 27.5 × 15.6 × 5.9 mm (Fig. 10).

MANTLE. Shell positioned at anterior third, body up to 4 times length of shell; mantle surface thickened, pustules or tubercles lacking; color brown, black, or gray, some mottled, with lighter areas in a radiating pattern (Fig. 11).

Dimensions of large preserved specimen: 70 × 50 × 32 mm (Fig. 15).

The shell is but slightly exposed in undisturbed living specimens; that in Figure 11 is a living specimen in a dish of sea water in which the mantle has retracted to expose the shell, as in preserved specimens. Figures 15 and 16 show two preserved specimens from another locality, one of which (Fig. 16) did not retract the middle fold to expose the shell.

RADULA. Rachidian tooth 1½ times broader than high (Fig. 18).

DISTRIBUTION AND OCCURRENCE. Uruguay (Figueiras and Sicardi, 1980), south to Tierra del Fuego, and the Falkland Islands; north in Chile to at least Pargua, Llanquihue Province (41° 47′ S) (LACM). Rocky intertidal and sublittoral zones, not uncommon.

TYPE MATERIAL AND LOCALITY. According to Dance (1966), the Strebel Collection was destroyed in World War II. Type locality: Lennox Island, SE of Tierra Del Fuego, Argentina.

MATERIAL. LACM, 4 lots, intertidal and sublittoral in the Gulf of Corcovado, at Pargua, Pumalin, and Islota Nihuel, Chiloe Province, Chile, collected by J. H. McLean, November 1975. 1 lot, intertidal, Puerto el Hambre, Strait of Magellan, Magellanes Province, Chile, J. H. McLean, November 1975. LACM, 4 lots, 5–20 m, vicinity of Isla de los Estados, E of Tierra del Fuego, Argentina, collected by P. Dayton on R/V HERO, November 1972 and May 1973. LACM, 1 lot, Bahía Laura, Santa Cruz Province, Argentina (ex MACN). MACN, 1 lot, Punta Norte, Peninsula Valdez, Chubut Province, Argentina (Fig. 13).

COMPARISONS. The shell of *Fissurellidea patagonica* is narrower than that of *F. megatrema* and the foramen proportionately smaller and more elongate. Shells are less concave on the anterior slope than in *F. megatrema*. The mantle surface differs in lacking the regular swellings and concentrated, darkly pigmented areas of that species. The shell is relatively larger compared to overall body size than in *F. megatrema*.

REMARKS. Strebel, followed by later authors, placed this species in *Megatebennus*, no doubt because of the relatively large size of the shell compared to body size. However, the bodies of the large specimens from Isla de los Estados, Argentina (Figs. 15, 16) are nearly as large as those of *F. megatrema*. One specimen (Fig. 12) even has a white appearing margin to the shell, as do some specimens of *F. megatrema*. The specimen in Figure 17 is unusually thin-shelled.

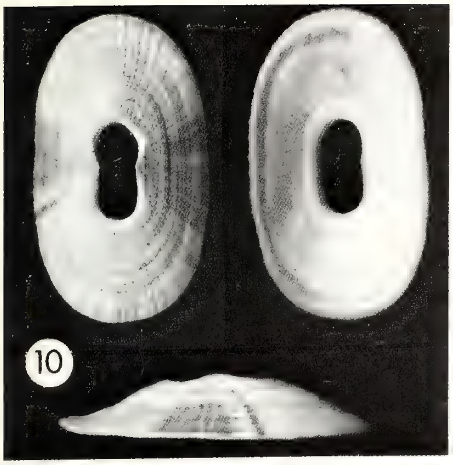
***Fissurellidea bimaculata* Dall, 1871**

Figures 19–25

Fissurellidaea [sic] *bimaculata* Dall, 1871: 132, pl. 15, fig. 7.
Megatebennus bimaculatus, Pilsbry, 1890: 183, pl. 44, fig. 94, pl. 61, figs. 10–12; McLean, 1978: 14, fig. 3.5.

SHELL. Elongate-oval, moderately thick, sides nearly parallel, anterior slightly narrower than posterior; ends raised relative to sides; sculpture of broad radiating ribs separated by deeply incised grooves; concentric sculpture of lamellar growth lines. Color light brown, rayed with gray or brown. Foramen central, ⅓ shell length, constricted in middle. Margin finely crenulate at edge, interior with rounded, projecting border.

Dimensions of large shell: 19.2 × 12.0 × 4.3 mm (Fig. 19).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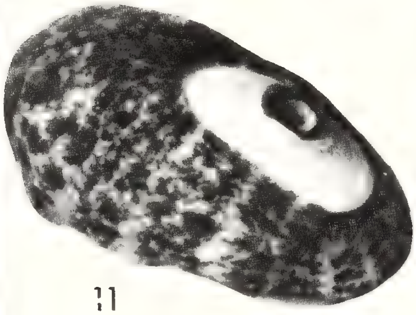
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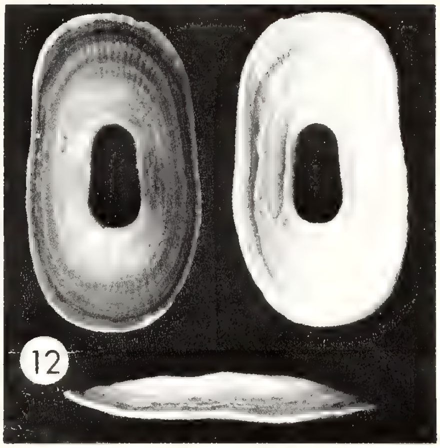
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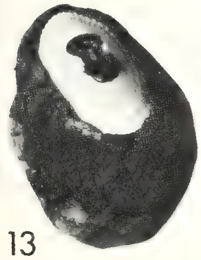
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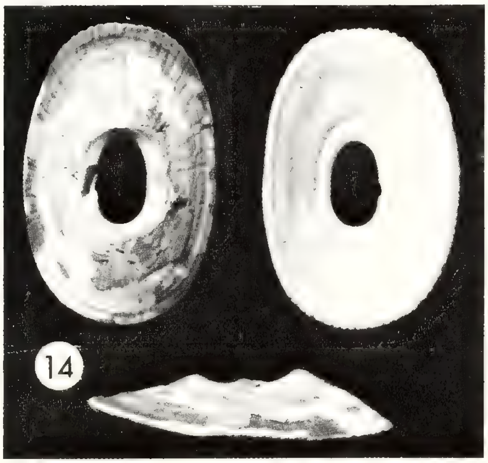
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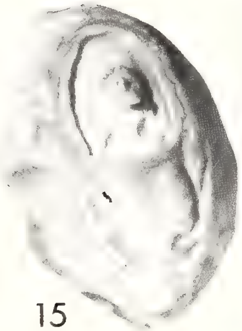
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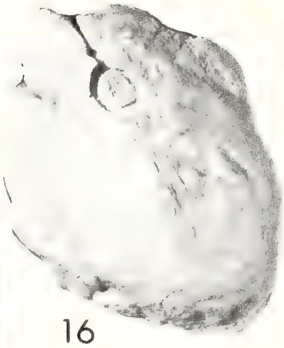
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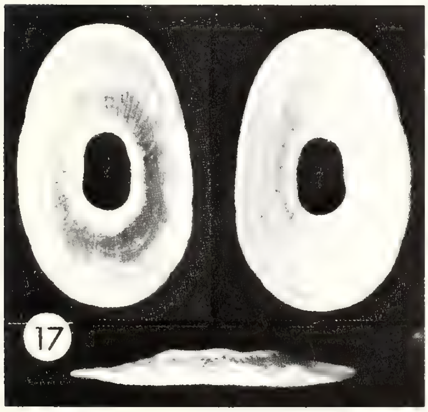
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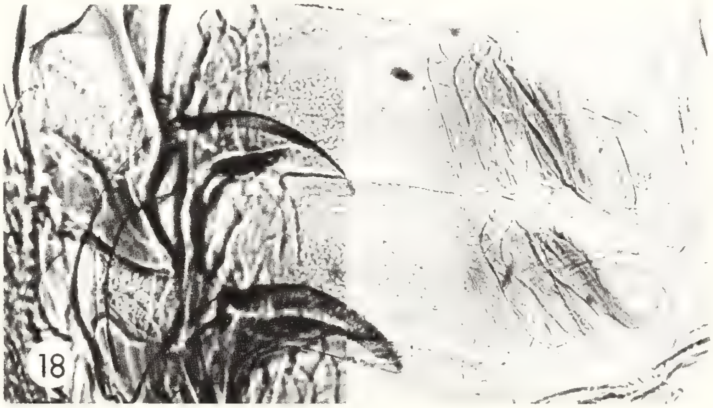
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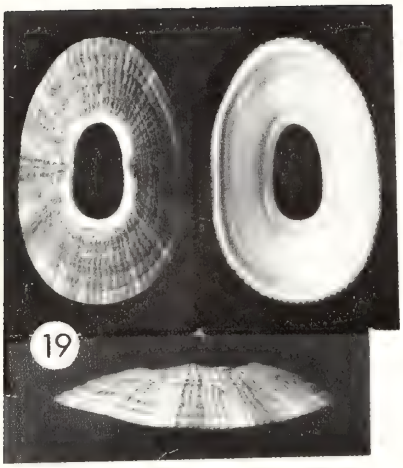
Figs. 10–18. *Fissurellidea patagonica.* **Fig. 10.** Shell. Islota Nihuel, Golfo Corcovado, Chiloe Province, Chile (42°38′ S, 72°57′ W), R. T. Paine, 7 November 1975. LACM 75-44, 27.5 × 15.6 × 5.9 mm. **Fig. 11.** Living specimen, anterior at right, same locality as Fig. 10. LACM 75-44, dimensions of now contracted animal: 41 × 24 × 17 mm. **Fig. 12.** Shell. 10 m, Bahia Tom, Magallanes Province, Chile (50°11.3′ S, 74°47.9′ W), P. Dayton, 2 November 1972. LACM 72-158, 28.3 × 15.7 × 4.5 mm. **Fig. 13.** Intact preserved specimen. Punta Norte, Peninsula Valdez, Chubut Province, Argentina (42°05′ S). MACN 8367, length 33 mm. **Fig. 14.** Shell from specimen in Fig. 15. Intertidal, Isla Garrido, Aisen Province, Chile (45°7.8′S, 74°24.8′ W), P. Dayton, 13 November 1972. LACM 72-162, 27.1 × 17.5 × 6.0 mm. **Fig. 15.** Preserved specimen with shell removed, same locality as Fig. 14 (shell in Fig. 14). LACM 72-162, 70 × 52 × 32 mm. **Fig. 16.** Preserved specimen, cut anteriorly to remove shell (shell in Figure 17). Same locality as Fig. 14. LACM 72-162, 62 × 41 × 28 mm. **Fig. 17.** Shell from specimen in Fig. 16. LACM 72-162, 24.9 × 15.4 × 2.8 mm. **Fig. 18.** Radular ribbon, light microscope preparation. Pargua, Canal de Chacao, Llanquihue Province, Chile (41°47′ S, 73°28′ W), J. H. McLean, 3 November 1975. LACM 75-30, horizontal width of field 1.5 mm, shell length 19.2 mm.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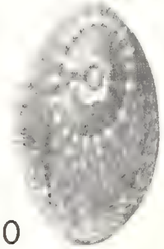
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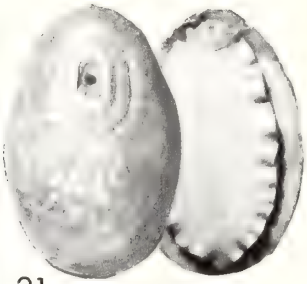
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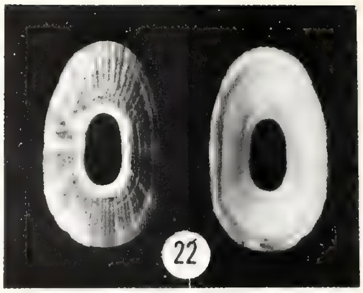
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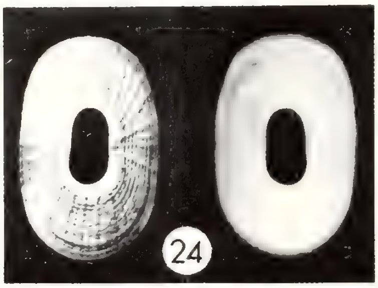
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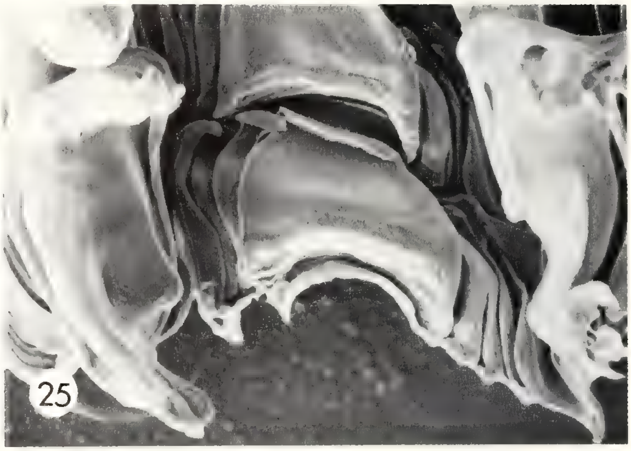
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Figs. 19–25. *Fissurellidea bimaculata*. **Fig. 19.** Shell. Albion, California (39°14.5′ N), J. H. McLean, 11 November 1962. LACM 62-15, 19.2 × 12.0 × 4.3 mm. **Fig. 20.** Preserved specimen with intact shell. Pt. Dume, California (34°00′ N), D. Cadien, 8 February 1971. LACM 71-37. 29 × 17 × 12 mm. **Fig. 21.** Preserved specimen with inact shell. Cayucos. California (35°27′ N), P. I. LaFollette, 11 December 1977. LACM 90795, 34 × 21 × 16 mm. **Fig. 22.** Shell, same locality as Fig. 19. LACM 62-15, 14.8 × 8.7 × 2.6 mm. **Fig. 23.** Preserved specimen relaxed and fixed in Bouin's fixative, shell dissolved. Carmel, California (36 32.5′ N), J. H. McLean, 14 October 1981. LACM 90805, 16 × 10 × 7 mm. **Fig. 24.** Shell. Bahia Adair, Sonora, Mexico (31°20′ N), E. Huffman, May 1935. LACM 31862, 8.7 × 5.6 × 2.1 mm. **Fig. 25.** SEM micrograph of radula, courtesy C. Hickman. Horizontal width of field 0.8 mm.

MANTLE. Body up to 3 times shell length; shell near anterior end. Mantle yellow, orange, red, gray, or brown; with rounded, projecting tubercles in radiating rows.

Dimensions of large preserved specimen: 33 × 22 × 13 mm (Fig. 21).

The middle fold of the mantle covers the entire shell in living specimens; in preserved specimens it retracts to partially expose the shell.

The smallest preserved juvenile specimen examined (LACM 90795) has a shell 3.5 mm in length; the apex is intact and the body is no longer than the shell.

RADULA. Rachidian tooth slightly broader (at base) than high (Fig. 25).

DISTRIBUTION AND OCCURRENCE. Dall Island, Southeastern Alaska (55° N), to Bahia Santiago, Colima, Mexico (19°26′ N). Fairly common south to at least Sacramento Reef, outer coast of Baja California, Mexico (30° N), from the intertidal zone to 30 m on undersides of rocks and overhangs. There are only two records further to the south: four specimens collected by E. Huffman at Bahía Adair, Sonora, in 1935 (Fig. 24) and one specimen collected at Bahia Santiago, Colima, Mexico, by Laura Shy in December 1966 (Shy Collection).

TYPE MATERIAL AND LOCALITY. Holotype, USNM 59273; type locality, Monterey, California.

MATERIAL. 78 lots are represented in the LACM collection from localities south to Sacramento Reef, Baja California.

REMARKS. This is the smallest member of the genus. The radiating rows of tubercles are similar to those of *F. megatrema* (compare Figures 3 and 23), which inescapably leads to the conclusion that the two species are congeneric.

Genus *PUPILLAEA* Sowerby, 1835

Pupillaea "Gray," Sowerby, 1835: 2 [validated in synonymy]. Type species (monotypy): *Fissurella aperta* Sowerby, 1825.

Pupillia Gray, 1840: 114, 147 [name only, invalid emendation of *Pupillaea* Sowerby].

SHELL. Moderately elevated; outline ovate rectangular, ends raised relative to sides; radial sculpture very subdued; foramen oval, from ⅓ to ½ shell length, interior callus ring narrow, muscle scar very narrow; shell margin not crenulate, pigmented exterior layer of the shell sharply offset from the white inner layer; interior border of margin narrow, not strongly projecting.

MANTLE. Body of animal 3 to 5 times longer than shell; mantle lobes thickened, enveloping shell and extending down to cover head and foot.

RADULA. Rachidian tooth 1½ to 2 times broader than wide.

REMARKS. The chief distinguishing feature of *Pupillaea* is the offset margin of the shell. Sowerby II (1862: 204) aptly described it: "The species . . . has the peculiarity of a depressed insertional rim, resembling that by which the valves of a *Chiton* are inserted into the surrounding integument." The outer fold of the mantle, which secretes the growing edge of the shell, must also be significantly different from that of *Fissurellidea.*

Pupillaea further differs from *Fissurellidea* in having more subdued radial sculpture, and a higher and more steeply sloping profile.

Until now *Pupillaea* has been considered monotypic, regarded by many authors as a subgenus of *Fissurellidea.* Here the Chilean species described as *Fissurelidea annulus* Odhner, 1932, is also allocated to *Pupillaea.* Although the shell of the latter is reduced, it also has the offset margin, subdued radial sculpture, and steep profile of the type species. The significance of these characters would be difficult to evaluate were there but a single species, but the existence of two markedly disjunct species, provides an incontrovertible argument for generic recognition of *Pupillaea.*

SYNONYMY. Pilsbry (1890: 180) and Wenz (1938: 85) credited the genus to Krause, 1848. However, Keen (*in* Moore, 1960: 231), following Dall (1915: 439), correctly credited the genus to Sowerby, 1835, who unknowingly validated a manuscript name of Gray in synonymy. Sowerby's entry (1835: 2, pl. 2, fig. 10) was this: "*Fissurella hiantula,* Lam. Conch. Illust. f. 10. Southern Africa. *Obs.* For a representation of this species Lamarck refers to Born Vign. f. F. which is the same as I named *F. aperta* in the Tankerville Catalogue. The following are therefore synonyms of this species, viz. *Fissurella aperta,* Tank. Cat. app. p. vi, *Pupillaea aperta*, Gray in Supp. to Beechey's Narrative." As discussed above under *F. megatrema,* the Born figure is discounted as a "type figure." The Sowerby (1825) name for the species *aperta* is therefore valid. Lamarck's *F. hiantula* is now used for a South African species of *Amblychelapas* on the strength of original specimens in the Lamarckian collection.

Although Sowerby (1835) quoted a listing of *Pupillaea* in 1835, Gray's "Molluscous animals and their shells, in Beechey's Voyage . . ." was not to be published until 1839 (Gray, 1839), and a "Pupillaea aperta" was not included. As Dall (1915: 439), noted: "*Pupillaea* Gray also appears for the first time in the Conchological Illustrations, cited from the unpublished notes of Doctor Gray on the Mollusca of Beechey's Voyage." Sowerby, however, is now the author of *Pupillaea.*

There is precedent for a familiar fissurellid genus validated in synonymy in the current usage of *Megathura* Pilsbry, 1890, which is now used for the large Californian *M. crenulata* (Sowerby, 1825). That generic name was first cited by Pilsbry (1890: 182) as "*Megathura californica* Nuttall MS," in the synonymy of "*Lucapina*" *crenulata.*

The synonym *Pupillia* Gray, 1840, was merely listed by Gray; no species were mentioned; the name must be considered an invalid emendation of *Pupillaea* Sowerby, 1835.

Fissurellidea and *Pupillaea* are here considered separate genera. A classification that equates the two at the subgeneric level will have to use the older *Pupillaea* as the nominate genus.

***Pupillaea aperta* (Sowerby, 1825)**

Figures 26, 27

Fissurella aperta Sowerby, 1825: vi; Reeve, 1849: fig. 39.

"*Fissurella hiantula* Lamarck," *of* Sowerby, 1835: 2, pl. 2, fig. 10 [with *F. aperta* in synonymy]. Not *F. hiantula* Lamarck, 1822.

Pupillaea aperta, Krause, 1848: 62, pl. 4, fig. 11; Sowerby II, 1862: 204, pl. 9, figs. 228, 229; Pilsbry, 1890: 180, pl. 44, figs. 6–8, pl. 62, fig. 9; Odhner, 1932: 304, fig. 41-1 [radula].

Fissurellidea (Pupillaea) aperta, Barnard, 1963: 288, fig. 21e [radula].

Fissurellidea aperta, Tietz and Robinson, 1974: 48, pls. 48c [shell], 49 [living animal]; Kilburn and Rippey, 1982: 36, pl. 6, fig. 13.

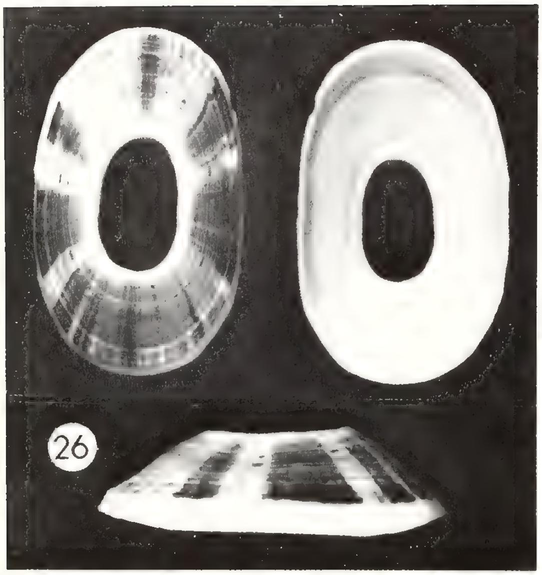
SHELL. Relatively large and thick, elongate-oval, sides steeply sloping, ends slightly raised; anterior slope longer than posterior and slightly concave, sides convex; ground color tan with dark gray rays. Sculpture of fine striae that form fine concentric lamellae under magnification. Foramen elongate oval, about ⅓ length of shell. Outer shell layer sharply offset from broad, white inner layer; muscle scar narrow, interior with narrow projecting margin.

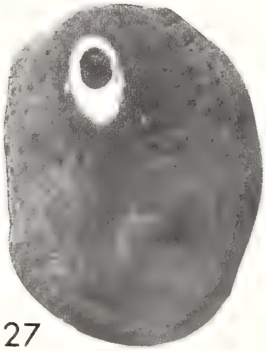
Dimensions of large shell: 39.0 × 24.4 × 10.3 mm (LACM 20206, Cape Town, South Africa). Maximum length 50 mm (Barnard, 1963).

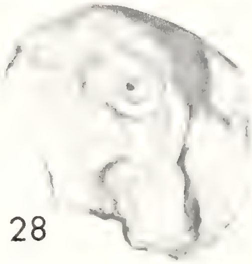
MANTLE AND FOOT. Mantle enveloping shell, head, and foot. "Black or brown to orange in color, with the sole of the foot orange" (Kilburn and Rippey, 1982). Krause's illustration (copied by Pilsbry) indicates a mottled pattern similar to that of the *Fissurellidea* species. Tietz and Robinson (1974) illustrated a specimen with a fully enveloped shell and scattered dark colored protuberances on the mantle surface.

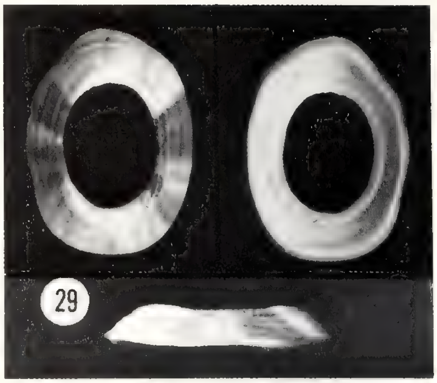
Dimensions of preserved specimen: 61 × 47 × 26 mm (Fig. 28). Largest preserved specimen: 110 × 80 mm (Barnard, 1963).

RADULA. Height of rachidian tooth about twice width









Figs. 26–27. *Pupillaea aperta.* **Fig. 26.** Beach worn shell. Strand, South Africa, D. W. L. Ackerman, January 1958. LACM 20246, 46.8 × 22.5 × 10.8 mm. **Fig. 27.** Intact preserved specimen. Intertidal, St. James, False Bay, South Africa. NM uncataloged, 61 × 47 × 26 mm. **Figs. 28–29.** *P. annulus.* **Fig. 28.** Preserved specimen with shell removed. Mehuin, Valdivia Province, Chile (39°23′ S), J. H. McLean, 31 October 1975. LACM 75-36, 42 × 32 × 16 mm. **Fig. 29.** Shell of specimen in Fig. 28. LACM 75-36, 10.1 × 7.7 × 1.7 mm.

at base (according to illustrations of Odhner, 1932, and Barnard, 1963); outer lateral tooth bicuspid. The rachidian is wider in the adult than in juveniles (Barnard, 1963).

DISTRIBUTION AND OCCURRENCE. Southern Africa, Namibia to Western Transkei, “lives on underside of submerged rocks in sandy crevices, at and below low-tide level” (Kilburn and Rippey, 1982).

TYPE MATERIAL AND LOCALITY. Type material was not recognized in the British Museum during my visit in September 1980.

MATERIAL. The LACM collection contains 6 shell lots and one specimen with dried animal, all from South Africa; three lots from the Natal Museum, Pietermaritzburg, have also been examined.

REMARKS. This is largest species in the *Fissurellidea* group; shells attain nearly twice the length of *F. megatrema.* The smallest shell examined (7 mm length, NM C.206) shows the offset margin. I expect that earlier juvenile stages will show an unmodified margin.

Pupillaea annulus (Odhner, 1932)

Figures 28, 29

Fissurellidea annulus Odhner, 1932: 292, fig. 34 [anatomy], fig. 41.2 [radula], pl. 5, figs. 1–3 [whole animal]; figs. 6–8 [shell]; Carcelles and Williamson, 1951: 253 [checklist only].

SHELL. Small, ringlike, oval, outline irregular; length of foramen over half length of shell, all slopes slightly less than 45 degrees from horizontal. Radial sculpture subdued, concentric sculpture of irregular, raised growth lines. Ground color buff, with lateral rays of gray. Margin sharp, not crenulated, offset from inner, white layer by angular groove.

Dimensions: 10.1 × 7.7 × 1.7 mm (Fig. 29); 13.5 × 9 × 1.5 mm (holotype).

MANTLE. Mantle enveloping shell, head, and foot. Surface of preserved specimen mostly smooth; color gray, with finely reticulating darker lines.

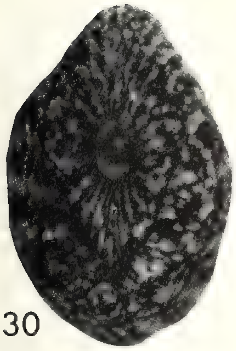
Dimensions of preserved specimens: 42 × 32 × 16 mm (Fig. 28); 72 × 63 × 35 mm (holotype).

RADULA. Rachidian tooth (as figured by Odhner, 1932) 1½ times broader than high; outer lateral tooth bicuspid.

DISTRIBUTION AND OCCURRENCE. Mehuin, Valdivia Province (39°23′ S) (LACM 75–36), to Melinca, Chiloe Province, Chile (43°54′ S) (type locality), rocky intertidal to 23 m. This species undoubtedly has a broader distribution in the Magellanic faunal province.

Chilean biologists have recently recognized this species in the fauna of southern Chile. Duarte, et al. (1980: 158) included it (as “*Fissurellidea*” *annulus*) in a study of caloric values among invertebrates from Valdivia, Chile (39°52′ S).

TYPE MATERIAL AND LOCALITY. Holotype, Uppsala collection. 23 m, Melinca, Islas Guaitecas, Chile (43°54′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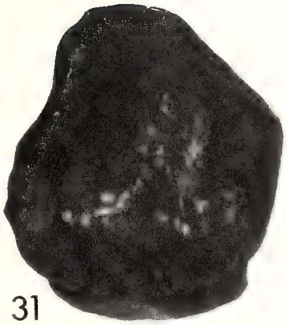
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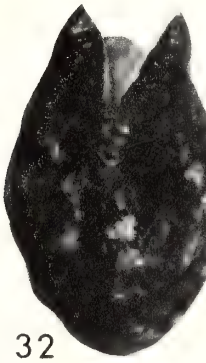
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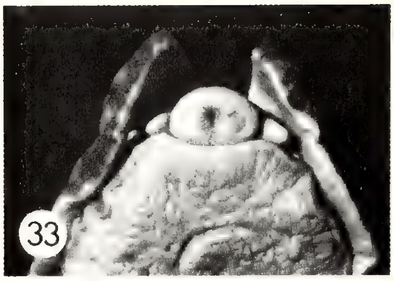
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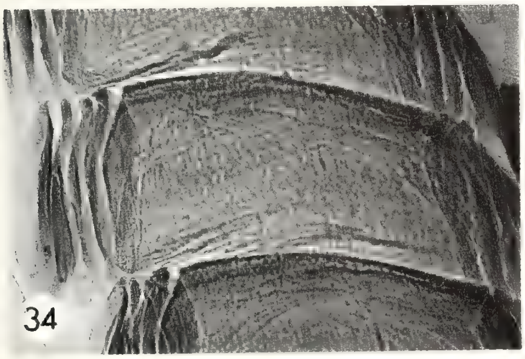
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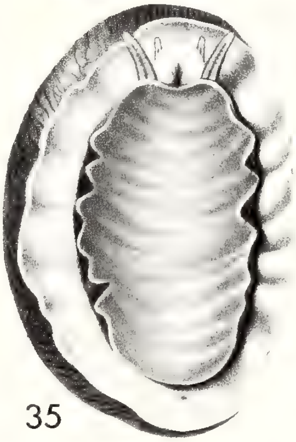
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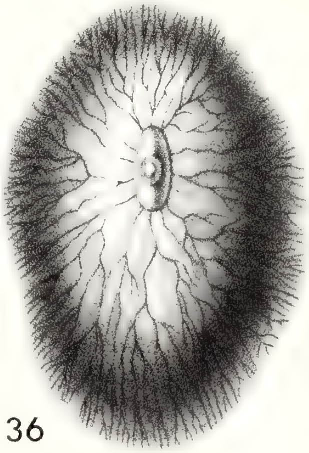
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Figs. 30–35. *Buchanania onchidioides.* **Fig. 30.** Preserved specimen. Isla Laitec, Chiloe Province, Chile (43°14′ S, 73°36′ W), J. H. McLean, 9 November 1975. LACM 75-47, 42 × 27 × 16 mm. **Fig. 31.** Preserved specimen, same lot as Fig. 30. LACM 75-47, 42 × 30 × 15 mm. **Fig. 32.** Preserved specimen, mantle cut anteriorly to demonstrate absence of shell, same lot as Fig. 30. LACM 75-47, 42 × 27 × 16 mm. **Fig. 33.** Ventral view of anterior of same specimen in Fig. 32, showing the gill tips lateral to the blunt cephalic tentacles on both sides of the snout. **Fig. 34.** Light microscope preparation of radular ribbon from specimen in Fig. 33. LACM 75-47, horizontal width of field 1.0 mm. **Fig. 35.** Copy of original illustration of Lesson (1830), ventral view; note large cephalic tentacles and gill tips projecting over snout. **Fig. 36.** Same, dorsal view.

S, 73°45′ W), collected by P. Dusen, May 1897 (Odhner, 1932).

MATERIAL. LACM 75-36, one specimen, rocky intertidal, Mehuin, Valdivia Province, Chile (39°23′ S), collected by J. H. McLean, 31 October 1975 (Figs. 28, 29).

REMARKS. Despite the greatly reduced shell, *Pupillaea annulus* has in common with the South African *P. aperta* the offset margin, steeply sloping sides, and subdued radial sculpture.

The ringlike shell of this species results from the slowing of growth at the margin, accompanied by a continued expansion of the foramen. Although small shells have not been seen, it is likely that they will have proportionately smaller foramina. The LACM specimen has a smaller foramen than the holotype, but is a smaller specimen overall; with further growth, the size of the foramen in this specimen would have increased.

Genus *BUCHANANIA* Lesson, 1830

Buchanania Lesson, 1830: 60. Type species (monotypy): *Buchanania ochidioides* Lesson, 1830.

Because this genus is monotypic, the generic and specific diagnoses and discussions are combined.

Buchanania onchidioides Lesson, 1830
Figures 30–36

Buchanania onchidioides Lesson, 1830: 60, pl. 14, figs. 4, 4D; Baker, 1938: 86, 88 ["a *nomen dubium*"].

SHELL. Lacking in mature specimens but probably present in juvenile stages.

MANTLE. Mantle thickened, enveloping head and foot on all sides, excurrent siphon ⅖ mantle length from anterior end. Elongate groove in mantle encircling foramen; groove extending ⅙ length of body, 1 mm in depth, lacking shell-secreting outer fold of mantle. Tips of ctenidia extending same length as (retracted) cephalic tentacles; side of foot with numerous, stubby epipodial tentacles. Color gray-brown with lighter mottling.

Dimensions: 42 × 27 × 17 mm (Fig. 32). Dimensions of original material: 80 × 68 mm (Lesson, 1830).

RADULA. Rachidian tooth twice as broad as high; outer lateral tooth bicuspid (Fig. 34).

DISTRIBUTION AND OCCURRENCE. Concepción, Concepción Province (36°42′ S) (type locality), to SE end Isla Chiloe, Chiloe Province, Chile (43°14′ S) (LACM) The species undoubtedly has a broader distribution in the Magellanic faunal province.

TYPE MATERIAL AND LOCALITY. Type material lost in the Paris Museum (Lesson, 1830). Type locality: Bahía Concepción, Chile, collected in February 1823.

MATERIAL. LACM 75-47, intertidal, Isla Laitec, off SE end Isla Chiloe, Chiloe Province, Chile, three specimens, collected by J. H. McLean, 9 November 1975 (Figs. 30–34). This is the only record subsequent to that of the two original specimens.

SYNONYMY. The identity of *Buchanania onchidioides* has remained a mystery until now, due primarily to the loss of the original specimens subsequent to the time that drawings were made on the expedition of the "Coquille." Based upon field notes and the illustrations (copied here, Figs. 35, 36), Lesson concluded that the specimens were related to "*Onchidia,*" now the family Onchidiidae. His generic name honored F. Buchanan, author of the genus *Onchidium* in 1800.

Authors treating the Onchidiidae (for example, Baker, 1938) have carried the name in lists of taxa in the family, but have not recognized nor further discussed the Lesson species. The generic name has also been burdened with misspellings and unnecessary replacements (*Buchannia* Gray, 1847; *Buchanaania* Gistel, 1848, and *Ephadra* Gistel, 1848, "substitute" for the latter; see references in Baker, 1938).

The rarity of the Lesson's "Voyage autour du monde. . . ." in library collections also helps explain how a carefully illustrated species could remain in limbo for over 150 years. Because few have access to the original description, I include here a complete translation of Lesson's account:

"It is only in a rather incomplete way that we mention this curious and unique mollusk, for which we sent two good specimens to the Paris Museum. In vain we have searched the anatomical collection with M. Laurillard, neither have we found it among the invertebrate animals preserved in alcohol, with M. Rousseau; they seem to have been misplaced. Only from notes taken in the field and a drawing of the animal made in life can we describe it for the researches of future travelers.

"*Buchanania* has the most in common with the onchidias, and some points in common with the doris and the phylidias. Like the onchidias, it has a large mantle, in the form of a shield, covering the entire foot and covering the head. As in the doris, the anus is dorsal, and as in the phyllidias, the gills are formed of leaflets placed in festoons (or scallops) along the two sides of the foot. The body of the specimen that we have illustrated reaches almost 80 mm in length, and the width about 68 mm. Its form is oval, its upper surface is very convex and rugose; the mantle excessively thick and fleshy, covering most of the foot. The foot is oval, rounded and free at the extremity, smooth or slightly striated over its surface. The shield of the mantle is leathery, papillate, pierced a little in front of center by a round hole, situated in the center of an oblong depression. The mouth is round, open under a fleshy flap, bearing on each side two pointed tentacles, contracted, and rather short, and two smaller, less prominent upper lobes.

"This mollusk has its mantle of dark cinnamon red, streaked with reddish brown. The thickened edge is on the underside yellow, tinted with red, and the foot is a very bright orange."

"We found it in February, 1823, at low tide, on a reef exposed for about two hours, later to be covered by a thick mass of water. The submarine bank is located at the entrance of the vast Bay of Concepcion, Chile" (Lesson, 1830).

It is apparent from the above that Lesson was a careful observer. Had he had opportunity to examine the preserved specimens upon return to Paris, he surely would have lifted the mantle in front to identify the smaller pairs of tentacles as fissurellid gills. He had made note of the epipodial tentacles and had interpreted them as gills, though these are not shown in his illustrations. In the preserved specimen in Figure 33, the tips of the gills project to the same extent as the cephalic tentacles.

The groove that surrounds the foramen of *Buchanania onchidioides* is clearly homologous to the larger groove containing the shell of *Pupillaea annulus,* but it is not as large as that of the latter, and it lacks the shell-secreting outer fold of the mantle that may clearly be seen in the groove of that species after removal of the shell. There is the possibility that specimens identified as *Pupillaea annulus* are but a developmental stage of *Buchanania onchidioides,* but that possibility seems remote, considering that my material of both species appears to be mature. Also, the gill tips in my specimen of *P. annulus* do not project as far as the snout.

CONCLUSIONS

One advantage of the limpet form is that of protection by means of clamping against the substratum. The loss of such capacity is a necessary consequence of shell reduction. All large-bodied fissurellids are unable to tightly adhere and are restricted to low-energy environments, where their prey organisms, sponges and tunicates, flourish. Here the fissurellids have a cryptic form, resembling their prey organisms. Indeed, their habits are more like those of the dorid nudibranchs, which they resemble, than like other limpets.

That the shell in adult members of the *Fissurellidea* group is vestigial, with virtually no function, has been said previously (see Ghiselin, et al. 1975). The truth of this statement may now be illustrated in *Buchanania*, which is comparable to *Fissurellidea* or *Pupillaea* in every respect other than lacking a shell.

The shell is of importance, however, to young stages of the *Fissurellidea* group, considering that juveniles have relatively large shells. Because there is a shell groove in the mature stage and because the species is like *Fissurellidea* in every other respect, it is evident that *Buchanania onchidiodes* must have a shell in its juvenile stage.

A description of juvenile *Buchanania ochchidiodes* would be of great interest, to discover how long it persists, and to see if the edge is rounded like that of *Fissurellidea*, or offset, as in *Pupillaea*. I expect it to be offset, in keeping with my hypothesis that *Buchanania onchidiodes* represents the final development in the trend toward shell loss seen in *Pupillaea annulus*.

ACKNOWLEDGMENTS

I am particularly grateful to those who made arrangements for my field work in Chile and Argentina. R. T. Paine, of the University of Washington, invited me to participate in his expedition to Chile in October and November 1975, for which expenses were partially underwritten by the National Science Foundation (DES 75-14378, R. T. Paine, principal investigator). W. J. Zinsmeister, Ohio State University invited my participation on Cruise 783 of the R/V HERO in Argentina in July 1978.

Other significant material was contributed by Paul Dayton, Scripps Institution of Oceanography, who collected *Fissurellidea patagonica* in southern Argentina in 1972 and 1973, and C. J. Risso-Dominguez, of Buenos Aires, who collected *Fissurellidea megatrema* in the vicinity of Mar del Plata, Argentina, 1964–1968.

Following my field work in Argentina in 1978 I examined the collections at the Museo Argentino de Ciencias Naturales, Buenos Aires, where access to the collection was facilitated by Martinez Fonte. Other specimens were loaned by William K. Emerson of the American Museum of Natural History.

Carole S. Hickman, University of California, Berkeley, provided the SEM radular illustration of *Fissurellidea bimaculata*. S. Stillman Berry of Redlands, California, loaned his copy of Lesson's "Voyage autour du monde. . . ." Jo-Carol Ramsaran of the LACM Malacology Section assisted with curatorial and library tasks. The LACM photographers and illustrators assisted with preparation of the figures.

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BURROWING ACTIVITIES OF *PERIPLOMA MARGARITACEUM* (LAMARCK, 1801) (BIVALVIA: ANOMALODESMATA: PERIPLOMATIDAE)

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ABSTRACT

Observations made on *Periploma margaritaceum*, from the Indian River, Florida, show that it uses its siphons as a bellows to cleanse the mantle cavity of sand and debris that enters during burrowing activities. Measurements of specimens of this hermaphroditic species from collections made throughout 1982 indicate that recruitment from spring spawning occurs during the fall. The species inhabits silty sand in shallow water and burrows into the substratum to a depth of a few centimeters. Fundamental differences exist between Periplomatidae and Laternulidae that involve anatomy and function of the siphons, and orientation of the animals in the substratum.

The Periplomatidae, a small family of marine bivalves, are world-wide in distribution (Rosewater, 1968). The valves are thin, fragile and have an intrinsic fracture through the umbos that proceeds ventrally for some distance and is buttressed with shelly material on the inner surface of the valves. Hinges are simple and no conventional teeth are present, their function being taken over by a spoon shaped chondrophore in either valve. A lithodesma usually extends transversely, from one valve to the other, behind the chondrophore. A ligament fits into a depression in each chondrophore further connecting the valves. The thin shell apparently does not offer much protection from predators, some populations showing a high degree of predation (Rosewater, 1980). *Periploma* apparently evidences "r-selection" and manages to exist as a biological entity through the production of sufficient numbers of young to replace those lost by predation or the natural death of aging populations (see discussion in Vermeij, 1978, pp. 170–173). The latter is an assumption, however, and little is known of the natural history and biology of most of these bivalves. This is because they are infaunal and when removed from their habitat are very shy and cryptic in behavior (Morse, 1919). Pelseneer (1911) gave one of the first reports on the anatomy of a periplomatid, describing *Periploma ovata* ? [sic], which was said to possess separate siphons, the excurrent being larger. Allen (1958, 1960) studied the anatomy and behavior of *Cochlodesma praetenue* (Pulteney, 1799) which he found buried in the substratum usually with the right side down, the incurrent siphon extending toward the surface, and the excurrent siphon directed posteriorly. Morton (1981a) summarized information concerning the subclass Anomalodesmata and proposed that families Thraciidae, Laternulidae, and Periplomatidae comprise the superfamily Thraciacea Stoliczka, 1870. Morton (1981b) extensively examined the biology and anatomy of another species of periplomatid, *Offadesma angasi* (Crosse and Fischer, 1864).

Because details of the natural history of most species of Periplomatidae remain unknown, observations on *Periploma margaritaceum* were undertaken at the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida, in 1982. This is the type species of the genus *Periploma* and serves as a pattern for studies on other species. The information obtained thereby is invaluable in carrying out a planned study on the systematics and zoogeography of the family.

MATERIALS AND METHODS

Collections: Collections of *Periploma* specimens were made in January, April, May, September and November 1982, at low tide (in depths of from 0.5–1.5 m), from grassy sand flats, near St. Lucie Inlet, Martin County, Florida (ca. 27°, 10′N; 80°, 11′W). Salinities varied from 25 to 35‰ depending on tidal flow [the locality is near the mouth of the St. Lucie River]. Method of collection was digging with a shovel to a depth of 15–20 cm, and sieving the substratum with a 0.5 mm nylon screen. Specimens captured were placed in sea water and returned to the laboratory for study. There they were maintained in aerated sea water at ambient temperatures (ca. 27°C) for a week or more while observations were made.

An attempt was made to utilize the mineral, cryolite, as a transparent substratum for observation of the animals *in situ*. While cryolite is an acceptable substratum for such active burrowers as *Mulinia lateralis*, it was not successful for *P. margaritaceum*, probably because its crystals were not ground fine enough. *Periploma margaritaceum* appears to prefer a substratum of fine, silty sand that will pass through a 202 μm screen.

Specimens were observed with a Wild Stereomicroscope in fingerbowls both with and without substratum. If placed on substratum they were allowed to lie on top for a period of time. Since usually no burrowing occurred with the specimens in that position, anterior ends of the clams were gently pushed into the substratum so that they were oriented in presumed natural beginning burrowing position (see Stanley, 1970, p. 99). Burrowing activities were usually initiated within a few minutes following the latter reorientation.

OBSERVATIONS

Habitat: *Periploma margaritaceum*, in the Indian River, Florida, inhabits grassy sand bars near St. Lucie Inlet. It lives buried in silty sand of a particle size less than 202 μm and at depths probably less than a few cm. They have been found in this habitat throughout the year.

Size-frequency: specimens were never abundant during the several occasions I searched for them at St. Lucie Inlet. A summary of the living specimens collected and their length measurements is given in Table 1. No individuals were found at that locality, living or dead, exceeding 10.2 mm in length, although only about 140 km north, at Cocoa Beach, Florida, specimens have been found reaching 14 mm (USNM 608799, 778145), and along the Gulf of Mexico coast, a length of over 30 mm may be reached (USNM 607127). Although specimens from the St. Lucie Inlet population are small in size, gonadal sections indicate they are sexually mature hermaphrodites, the sexual condition typical of anomalodesmatans according to Morton (1981a,b), and Boss (1982). One of the specimens collected in April 1982 contained large numbers of mature ova.

Measurements and statistics shown in Table 1 give a general indication of population changes over the year. Mean length appears to be greatest in May, when optimum temperatures for spawning may be reached. Recruitment of smaller individuals was noted in September and general increase in mean length seems to occur in late November. The mean width/length ratio of 32 specimens collected in November was 0.61.

Anatomical notes: gross anatomy of *P. margaritaceum* is similar to that of *Offadesma angasi* (Morton, 1981b). A small fourth pallial aperture is located just ventral to the incurrent siphon. The mantle is fused from that point to the small pedal opening located anteriorly.

Habits: when placed in a dish of clean seawater, without substratum, the valves of *P. margaritaceum* either remain closed or there may be protrusion of the translucent, spade-shaped foot which probes the bottom of the dish in an attempt to burrow (see Plate 1, Fig. B).

Individuals refuse to burrow in a substratum composed of particles larger than 202 μm or unfamiliar consistency (cryolite, see Materials and Methods). This is probably due to the fact that it causes damage or "discomfort" while passing through the mantle cavity and siphons during burrowing (see below). When placed in a dish of seawater that also contains several centimeters of the silty sand substratum, the foot is protruded and the animal may attempt to bury itself. If it is not successful, and the anterior end is then mechanically introduced into the substratum at a 45° angle, burrowing usually commences and the animal may be completely buried within a few minutes.

The burrowing sequence is as follows: individuals penetrate at an angle by introducing the foot into the substratum and gain a purchase with its enlarged, spade-shaped end. The shell is subsequently pulled down in shallow increments. Specimens removed from the substratum at this time have the mantle cavity packed with silty sand substratum. When the posterior end of the clam's shell is approximately level with the surface of the substratum, and the mantle cavity is packed with sand, burrowing ceases momentarly and the excurrent and incurrent siphons are protruded slowly. The globular excurrent siphon is larger in diameter than the incurrent siphon and bears from 6–9 tentacles surrounding its elongate opening. The incurrent siphon is considerably smaller in diameter and more elongate. Its opening also is surrounded by tentacles. I believe that the tentacles of *Periploma* serve a tactile sensory function, as no eyes have been observed as were found in

Table 1. Comparison of length measurements of live collected *Periploma margaritaceum* from St. Lucie Inlet, Florida, January–November 1982 (N number of specimens in sample; Range L mm = Range of lengths of all specimens in sample measured in millimeters; M = Mean = average of all specimens measured/number of specimens in sample; SD = Standard Deviation from the Mean; V = Variance).

	Jan	Apr	May	Sept	Nov	
N	4	22	10	15	19	13
Range L mm	3.0–7.7	3.0–9.6	6.5–9.0	4.5–9.8	4.2–10.2	5.7–8.9
Mean	5.8	6.6	7.8	6.2	6.2	7.2
SD	1.8	1.8	0.8	1.6	1.4	1.1
V	3.4	3.4	0.6	2.6	1.8	1.2

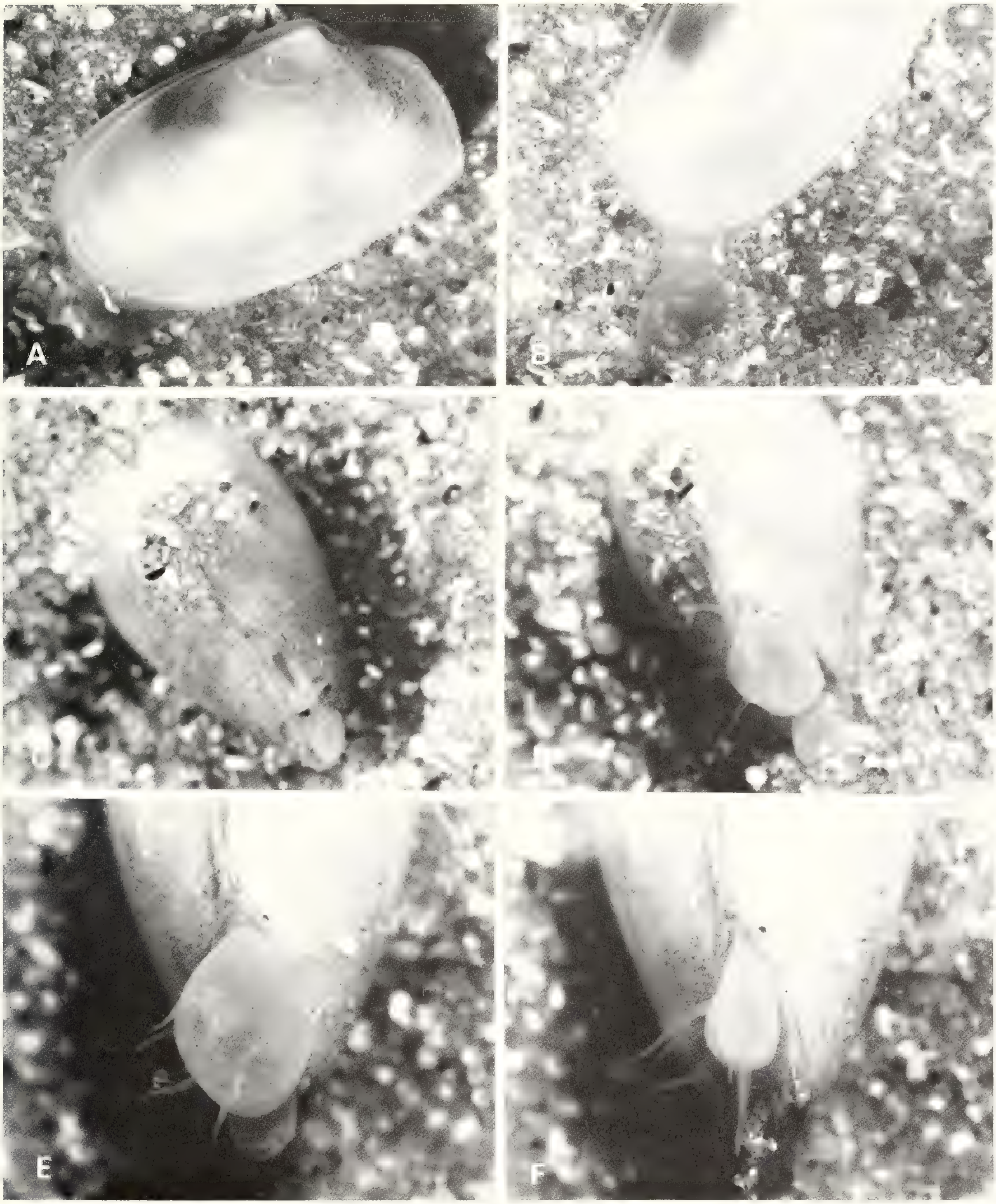

Plate 1. Figs. A–F. Stages in burrowing of *Periploma margaritaceum*, from St. Lucie Inlet, Martin County, Florida, collected April 27, 1982, showing activities of the siphons. A. Individual lying on right valve with foot protruding slightly antero-ventrally from mantle pedal aperture (note intrinsic fracture in uppermost [left] valve at umbo). B. Foot digging into substratum, showing enlarged tip. C. Partially buried, siphons beginning to protrude (note elongate opening of excurrent siphon with 2 tentacles showing). D. Siphons more fully protruded (note contrasting shapes of globular excurrent, and tubular incurrent siphons). E. Excurrent siphon expanded to near maximum; 8 tentacles showing. F. Excurrent siphon contracting (note sand grains being blown out of more ventral incurrent siphon). (Specimen measures 7 mm in length; photos by J. Rosewater).

Laternula by Adal and Morton (1973), nor were they noted in *Offadesma angasi* by Morton (1981b).

Behavior of siphons in cleansing mantle cavity: siphons are initially protruded when the clam is almost completely covered by substratum and only the posterior end of the shell is visible. The excurrent siphon becomes considerably expanded and bulbous; the incurrent siphon also is extended. The opening of the excurrent "bulb" is closed when it has reached maximum size. Next a contraction of the excurrent siphon occurs, followed by a series of contractions of the siphon that expell water and accumulated sand and debris out through the incurrent siphon, clearing the mantle cavity. The animal then resumes burrowing and disappears into the substratum. It then reopens a single "respiratory-feeding" aperture in the sand through which there is periodic expulsion of sand grains via a water current. (see Plate 1, Figs. A–F, depicting the series of burrowing stages).

DISCUSSION

The population of *P. margaritaceum* at St. Lucie Inlet has a mean length that appears small for the species (individuals collected over an 11 month period averaged 6.6 mm in length; see Observations and Table 1). These individuals are reaching sexual maturity, as indicated by gonad sections and examination of specimens having mature ova (April 1982). Available size-frequency data indicate that St. Lucie individuals reach sexual maturity in late spring, with newly settled individuals becoming apparent in November. These data indicate a one year life history. Further data are required before definitive statements can be made regarding the life history of *P. margaritaceum.*

Observations on living periplomatids have been rather rare probably due to their subtidal habitat and cryptic habits. Analyses of habitats have been made on only a few species. Allen (1958) reported *Cochlodesma praetenue* (Pulteney, 1799) to occur in fine gravel, sand and muddy sands from spring low tide line to depths of 60 fathoms, although most commonly the species lives in sand and sandy gravel in sheltered areas just below low water. There individuals are buried to a depth of 7 cm below the surface of the substratum where they lie with one valve down, usually the right one. Harry (1976) found *Periploma orbiculare* Guppy, 1882, to occur in substrata of more than 50% mud/sand in Lower Galveston Bay, Texas. Littleton (1982) analysed distributions of *P. orbiculare* and *P. margaritaceum* in Matagorda Bay, Texas. He found them to be well separated ecologically based on the types of sediments in which each lives: *P. orbiculare* generally inhabited sediments at mid bay composed of from 80 to 100% mud at a range of depths from 1.52 to 3.66 m; *P. margaritaceum* occurred in sediments nearer shore composed usually of greater than 71% sand and at a range of depths from 0.61 to 3.66 m (but usually shallower than the deepest depth cited). Since the shell of *P. orbiculare* is more rounded in outline than that of the rather wedge-shaped *P. margaritaceum,* it appears that there is a correlation between shell shape and habitat: softer sediments allowing clams with a less streamlined-shaped shell to burrow more easily, whereas those with wedge-shaped shells can penetrate a more dense, sandy substratum with greater ease. Morton (1981b) found *Offadesma angasi* in several localities in North Auckland, New Zealand, living in shallow water at a depth of 7–8 cm in firm sand, always lying on its left valve, inclined at an angle of 20°, with both siphons extending to the surface of the substratum. In this study *P. margaritaceum* occurred living in silty sand, probably quite similar to its habitat as previously described by Littleton (1982). It seemed to prefer a particle size of less than 202 μm for burrowing and this substratum was provided for my laboratory observations.

Burrowing activities of bivalves, as summarized by Stanley (1970), generally consists of several stages: beginning with 1. the foot probing downward into the substratum and enlarging at its tip; 2. closing of siphons; 3. forcible adduction of valves with resultant ejection of water from the ventral mantle opening; 4. retraction of the foot which pulls the shell downward into the substratum; 5. relaxation of the adductor muscles allowing the valves to gape; and finally, 6. a resting stage prior to the renewal of the cycle. In many mollusks strong shell adduction ejects a water current out the pedal mantle opening forcing the substratum away from the anterior portion of shell at the same time the foot is pulling the animal downward. This has been observed clearly in such strong burrowers as the surf clam, *Spisula solidissima* (Dillwyn, 1817) (Ropes and Merrill, 1966).

In contrast with the surf clam, periplomatids are sluggish burrowers. Morse (1919) pointed out that *Anatina papyratia* Say [sic] (= *Periploma fragile* Totten, 1835) is very timid and sluggish and performed little while he observed it. He was able to observe that its siphons are separate, and noted that the excurrent siphon was inflated to twice the diameter of the incurrent siphon. Tentacles surround both siphonal openings. Allen's (1958) description of *Cochlodesma praetenue*, a related form, showed similarities and gave more details. That species lives buried, usually on its right side, with the incurrent siphon extending upward toward the surface of the substratum, and the excurrent siphon extended posteriorly (horizontally) into the substratum. Both siphons form mucous lined tubes. Unpublished observations by H. W. Harry (*in litt.*, 1967) show the gross anatomy, mantle and siphon characters of *Periploma orbiculare* Guppy, to be very similar to other periplomatids, except that he could find no ventral opening in the mantle. *Thracia pubescens* (Thraciidae) has been reported by Forbes and Hanley (1853, pp. 219–238), and Yonge (1937), to have similar appearing siphons to those of Periplomatids, except that both siphons of *Thracia* extend to the surface of the substratum, and two siphonal holes are found at the ends of the substantial mucous-lined tubes. It was suggested by Forbes and Hanley (1853) that the siphons of *Thracia* are used to eject "water and 'rejectamenta' with greater force" [from the mantle cavity]. The latter was questioned by Yonge (1937) who believed the peculiar appearing siphons fit them only for tube formation. Morton (1981b) reported that *Offadesma angasi* is unable to reburrow once it is removed from its substratum. He noted peristaltic waves from base to tip of its siphons, possibly an indication the species is capable of some of the activities observed in the siphons of *P. margaritaceum.* The siphonal anatomy of most periplomatids described to date appears grossly similar to that of the siphons of *Periploma margaritaceum* which help that clam burrow and clear its mantle cavity through muscular, bellows-like contractions. The extensive mantle fusion noted in this species, and the anteriorly located small pedal aperture, undoubtedly contribute to its ability to close off and flush the mantle cavity. The function of the fourth pallial aperture is not known. It possibly may serve as a 'relief valve' when the mantle is under internal pressure during contraction of the excurrent siphonal bellows (see Observations).

Valves of both Thraciidae and Periplomatidae are very fragile, and subject to breakage. This is common to Pandoracea in general (Taylor, Kennedy and Hall, 1973, p. 282, table 20). As suggested by Prezant (1981) there are correlations evident between shell structure, habitat and the evolution of bivalves. Morton (1981b) recommended separate superfamily status for Periplomatidae, Laternulidae and Thraciidae: Thraciacea Stoliczka, 1870, based on similarities in their shells and ligaments. Shells of Periplomatidae are buttressed internally to the intrinsic crack in their valves at the umbos, but it is doubtful they could survive the repeated adductions performed by other bivalves in burrowing and in ejecting pseudofaeces and other foreign matter from the mantle cavity.

Adal and Morton (1973) and Morton (1973, 1976) have analysed the functional anatomy of Laternulidae, a family often considered to be close in relationship to Periplomatidae. Greatest similarities appear to be related to the presence of intrinsic fractures at the umbos of both valves, buttressing of the fractures with shelly material on the inner surfaces of the valves, the shape of the chondrophore and the possession of a lithodesma. Some very basic differences between the two families are that the siphons of Laternulidae are joined and non-retractable, while in Periplomatidae they are separate and retractable; siphonal eyes were reported in *Laternula* by Adal and Morton (1973), but have not yet been observed in periplomatids; there is a permanent posterior shell gape in Laternulidae, but the posterior shell closes tightly in Periplomatidae; laternulids are oriented vertically in the substratum, while periplomatids are oriented horizontally.

On the basis of his analysis of the shells of Laternulidae, Morton (1976) proposed that the vertical umbonal fractures permit the shell to be adducted like four partly disjointed functional valves, allowing the shell to close and mantle-siphonal currents to be generated. My observations on *P. margaritaceum* and other periplomatids indicate a very basic difference from Laternulids in the function of the siphons and generation of these currents.

I suggest that the described siphonal activities of periplomatids replace the muscular adduction used in such forms as *Spisula*. The current generated by the bellows-like excurrent siphon of *Periploma margaritaceum* flushes the mantle cavity of sand and debris that enters the pedal mantle opening during foot probing/burrowing activities, and by the same means helps remove substratum from the clam's path. A forceful anteroventrally directed current, such as the one that helps bivalves like *Spisula* displace the substratum and excavate their burrows, is not needed in *Periploma.* The fragile valves of *Periploma* are thus preserved from being fractured further and burrowing is achieved. Since only one siphonal opening penetrates the substratum following burrowing, it is presumed that *P. margaritaceum,* like *Cochlodesma praetenue* [observed by Allen (1958)], extends only its incurrent siphon toward the substratum surface, while its excurrent siphon extends horizontally and continues to perform periodic bellows-like actions to cleanse the mantle cavity during further burrow excavations. Additional observations of these activities utilizing a transparent substratum are planned to verify these interpretations.

The bellows-like activities of *Periploma* siphons function both in burrowing and cleansing of the mantle cavity of the "rejectamenta" referred to by Forbes and Hanley (1853), which would include pseudofaeces. This siphonal activity, in which water is passed retrograde to the ordinary respiratory-feeding current, into the mantle cavity via the excurrent siphon and carries sand and debris out the incurrent siphon, is readily seen in other bivalves when pseudofaeces are expelled.

The fact that these siphonal activities have not been observed in periplomatid species other than *P. margaritaceum* is surprising since most species studied have similar siphonal anatomies (Pelseneer, 1911; Morse, 1919; Allen, 1958; Harry, *in litt.*; Morton, 1981b). It is quite possible that younger individuals are most active insuring more rapid establishment of settling populations. Older individuals may become more sluggish, but *P. margaritaceum,* at least, will reburrow and perform siphonal activities readily if encouraged by partially imbedding anterior ends in suitable substratum. These siphonal activities may be interpreted as an adapation to life in a soft sandy-mud substratum.

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FUNCTIONAL MICROSTRUCTURE AND MINERALOGY OF THE BYSSAL COMPLEX OF *ANOMIA SIMPLEX* ORBIGNY (BIVALVIA: ANOMIIDAE)

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ABSTRACT

The calcified byssus of *Anomia simplex* Orbigny is produced by a modified byssal gland composed of a series of thin tissue folds. The biogenically produced calcitic byssus is composed of tightly packed lamellae that in turn make up a central, cylindrical core. This core, aligned dorso-ventrally, has a flared byssal attachment surface directed toward the hinge. The calcified lamellae are deposited upon organic threads or sheets. The attachment plaque is also deposited upon an organic layer that may act as a nucleation site and adhesive zone for attachment of the bivalve to the substratum. Small aragonitic spindles typically cover portions of the calcitic byssus. These spindles are likely inorganic in origin and may be a typical mineralogical precipitation upon molluscan calcified structures.

Many bivalve molluscs possess structurally and physiologically complex byssal glands that produce proteinaceous attachment threads. Best known of these bivalves are the epifaunal Mytilacea (Waite and Tanzer, 1981), but byssate molluscs include members from a wide range of higher taxa (egs. Arcacea, Pectinacea, Pandoracea). Yonge (1962) surveyed byssal glands in bivalves and concluded that the presence of an operative byssal gland in adults might be paedomorphic. Most adult anomiacean bivalves also retain a well developed byssus with which they permanently attach to hard substrata. The anomiid byssus, however, is not proteinaceous but instead is composed principally of calcium carbonate. This stout, columnar attachment structure passes from a modified byssal gland through a dorsal byssal notch in the right valve to the substratum. Morton (1979) suggested that the byssal threads of *Anomia* have coalesced "into a calcified cable. . . ." This is difficult to distinguish at the light microscopical level, and although shell microstructure of various members of the Anomiidae has been examined (Wada, 1963; Taylor et al., 1969), no comparable study of the calcified byssus has been published.

In conjunction with their microstructural studies, Taylor et al. (1969) examined shell, but not byssal, mineralogies. With the exception of aragonitic myostracum and ligamental needles, the entire shell of all species of *Anomia* examined by the latter authors was reported as calcitic. Carter (personal communication, 1983) notes that *A. simplex* has a well developed aragonitic crossed-lamellar structure as a very thin interior layer. Mineralogy of the calcified byssus had been left undetermined.

In the Bivalvia the two most common calcium carbonate allomorphs are calcite and aragonite. If we limit our discussion to these two morphs, it might be hypothesized that anomiid byssi are composed of aragonite, the "stronger" and more common of the two morphs (Milliman, 1974). In support of this hypothesis is the fact that aragonite is more typical of molluscan attachment layers [egs. ligostracum of Ostreidae (Carriker and Palmer, 1979), myostracum (Taylor et al., 1969)]. The inner surface of the byssus of Anomia is not only the face for addition of new calcareous material, but also the internal region for byssal anchorage or attachment. In fact, the byssus of *A. simplex* is principally composed of calcite.

This research was undertaken to explore the functional microstructure and mineralogy of the byssus of *Amonia simplex* Orbigny.

METHODOLOGY

Specimens of *Anomia simplex* were collected in December 1980 from along Bowmans Beach, Sanibel Island, Florida. These specimens, having a mean length of 25 mm, were found attached to single valves of *Argopecten gibbus* (Linné) or *Chione cancellata* (Linné). Typically, live anomiids were attached to the internal surface of a single valve substratum and often conformed to the shape of the "host" valve. All specimens were immediately preserved in 70% ethanol.

Anomiids were carefully separated from their substratum; displacement of their valves usually resulted in retention of calcified byssi on "host" shells. This allowed easy

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mounting of byssal specimens on aluminum scanning electron microscopy stubs. Byssi and supportive fragments of attached substrata were placed in a 30% solution of commercial Clorox (sodium hypochlorite) for three hours to dissolve primary organic deposits. Specimens were then washed in distilled water and dehydrated in a graded series of ethanols through absolute ethanol. Several changes of absolute ethanol over several days, followed by an eight-day stay in a 60°C drying oven insured dry specimens. Some byssi, as well as pedal and byssal gland soft tissues, were critical point dried after ethanol dehydration using carbon dioxide as a direct transfer agent in a Denton DCP-1 critical point drier.

Mounted specimens were coated in an argon environment with a thin layer of gold in a Polaron SEM Coating Unit E5100, and examined at 30kV in an AMR 1000 scanning electron microscope.

Mineralogical analyses were carried out using Feigl solution (Milliman, 1974) and X-ray diffraction. Feigl solution is an easy and fairly accurate method for quickly determining the two primary biological calcium carbonate polymorphs. The stain reacts rapidly with aragonite by dissolution of the mineral followed by precipitation of MnO_2 and Ag°, staining aragonitic deposits black (Carter, 1979). Calcite, on the other hand, is less soluble and resists staining. Mineralogical staining was verified by X-ray diffraction. For the latter, 2–4 byssi were ground to a fine powder in a glass tissue grinder, mounted on double stick tape on a glass slide and analyzed on a General Electric XRD 700 X-ray diffraction unit.

Histological sections of 70% ethanol fixed foot and byssal gland were obtained by embedding specimens in paraffin wax (m.p. 56.7°C) and sectioning at 7 μm. Sections, mounted on albuminized slides, were stained with toluidine blue or a modification of the Pantin trichrome stain (Prezant, 1979). Fractured, non-Cloroxed byssi were also stained with toluidine blue.

All figures are scanning electron micrographs unless otherwise indicated.

RESULTS

Byssus microstructure

The byssus of *Anomia simplex* is a columnar pillar, composed of a series of tightly packed lamellae, that emerges from a modified byssal gland, passes through a byssal shell notch in the right valve and attaches by way of an expanded plaque to a hard substratum (Figs. 1–3).

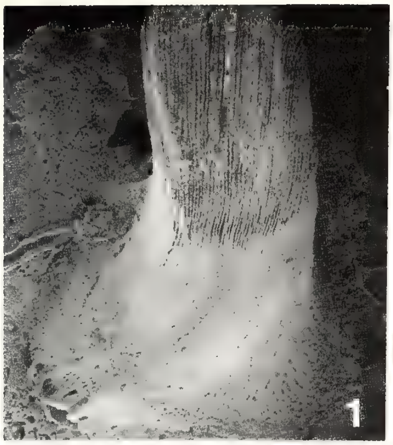
The byssus emerges anatomically dorsally through the byssus notch of the right (bottom) valve just beneath the hinge. Usually the byssus angles away from the shell ventrum. The column is thus aligned dorso-ventrally and has a flared byssal surface leading toward the hinge. A clam about 25 mm long has a byssus between 5–6 mm long and 1–2.5 mm in diameter. Curvature or angularity of the byssus dictates variations in vertical height. The direct vertical height (i.e. height from substratum to uppermost portion of byssus in a normal plane) rarely exceeds 2.5 mm (Fig. 4).

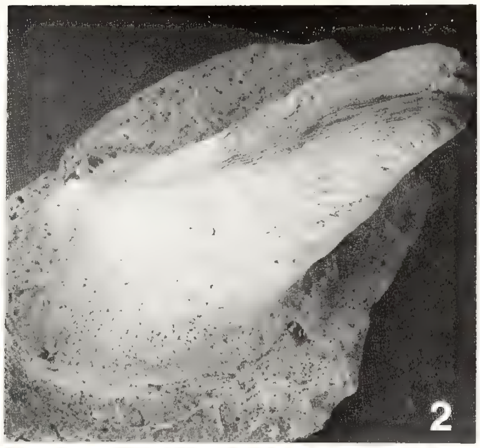
The upper surface of the byssus, which faces the left upper valve, reveals the lamellar nature of the byssus (Fig. 5). These lamellae remain, at their surfaces, in direct contact with the byssal glandular region of the foot. The lamellar structure of the byssus gradually tapers as the folds approach the basal portion of the byssus [i.e. the region of external attachment to substratum] (Fig. 6). Eventually the byssus flares dorsally into a basal plaque that has a superficially fine granular appearance at low magnifications (Figs. 1, 7). The morphologically ventral portion of the byssus resembles the relatively homogeneous structure of the plaque at low magnifications (Fig. 4).

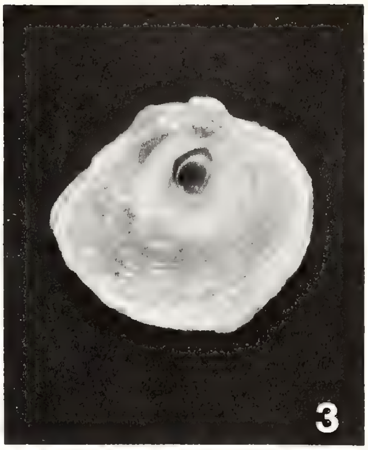
Closer examination of the plaque reveals a pitted surface with ovoid and "comma" shaped pores (Fig. 8). These may be a natural consequence of incomplete calcification in this basal area and not the result of dissolution or external biogenic forces. The flared dorsal periphery of the plaque molds itself tightly over the substratum surface (Figs. 1, 7–9). This area of merger appears to be one of irregular crystal growth with a heterogeneous leading edge (Fig. 9). Original growth in these areas is of a fine structure that produces irregular growth patterns discerned only at higher magnifications (Fig. 10). Under a dissecting microscope the basal periphery of the byssus appears as a thin brown ring. This is reminiscent of an organic deposit, and the fine, smooth structure of this area under the scanning electron microscope also supports a probable organic nature of this deposit. The brown deposit fills the peripheral gap around the substratum outlining the byssal notch but not covered by the central calcified byssus per se. Calcium carbonate deposits, reminiscent of a leading zone of nacreous growth, appear to be laid down upon an organic sheet (Fig. 9; s). Incipient growth covering this region, however, is substructurally more of a calcified, granular homogeneous type (Fig. 10) rather than a true nacre.

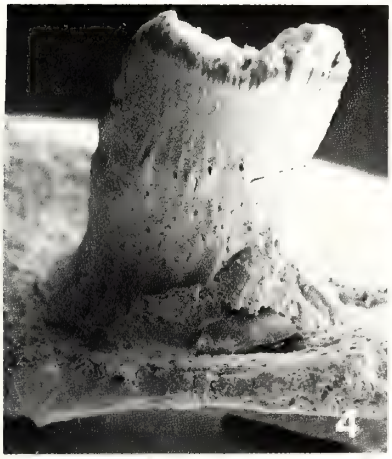
The ventral portion of the byssal column may also show irregularities at higher magnifications. A superficially heterogeneous structure results from numerous small ovoid or spindle-shaped granules (Fig. 11). These granules, which are not always present and sometimes irregularly dispersed, may be secondary, inorganic deposits. The largest spindles seen in this area were less than 5 μm long. Orientation of these spindles was irregular but many were arranged normal to the face of the ventral byssal surface.

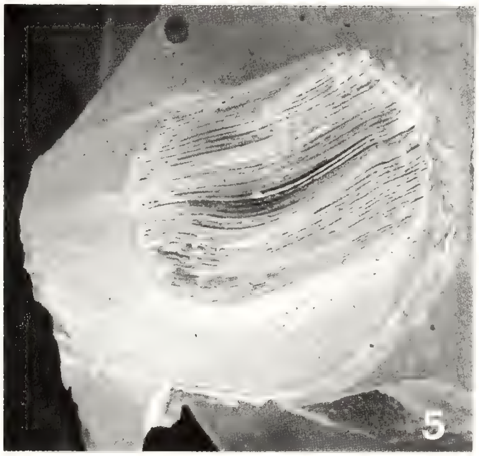
The uppermost, ventral region of the byssus suggests the lamellar nature that composes the entire anterior surface. At the apical region of the ventral byssus the structure breaks down into a series of apparent ridges (Fig. 12). Examination of the byssus in this region (Fig. 13) reveals that the lamellae are the basic growth structure for the entire complex and in regions where the lamellar structure does not show, it has been obscured by secondary growth, fusion, or dissolution. Just beneath the obvious lamellar pattern of the byssus in this area are hints of slight ridging (Fig. 13). The apical

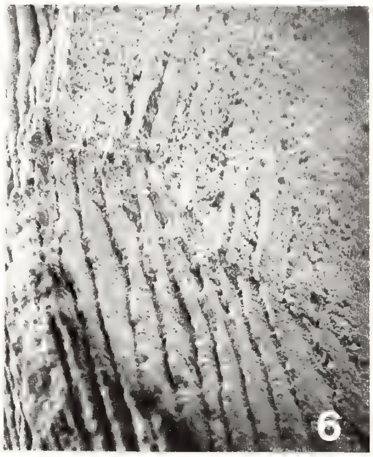


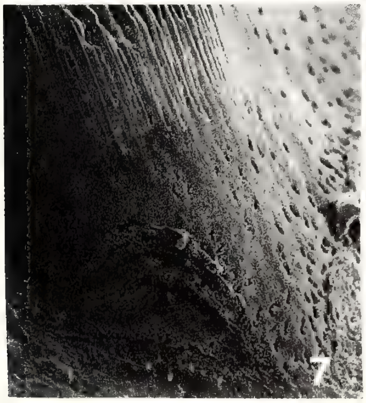


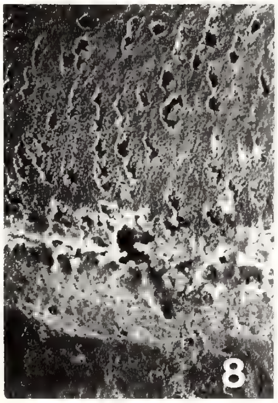


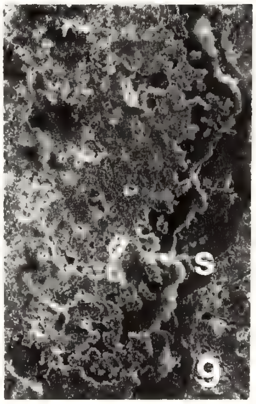












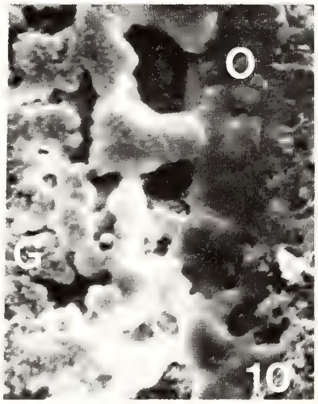
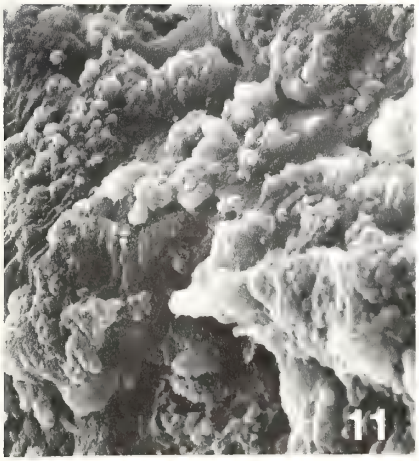
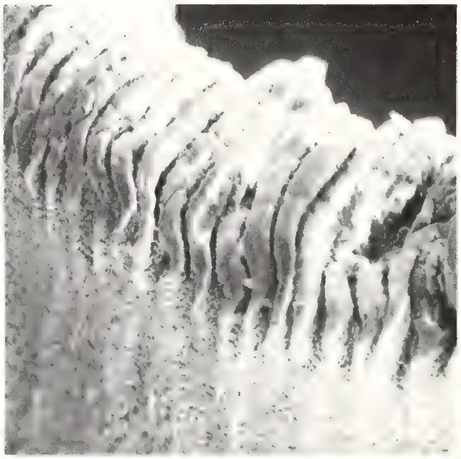
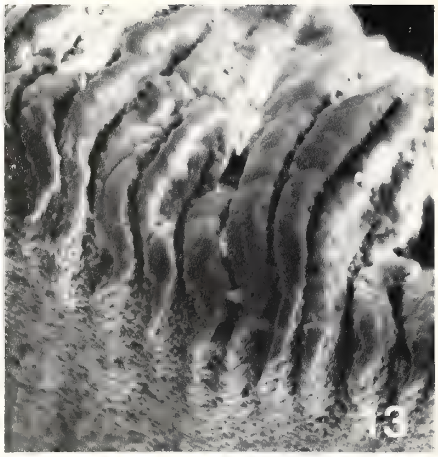
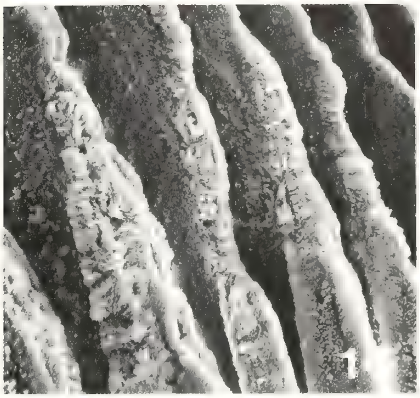


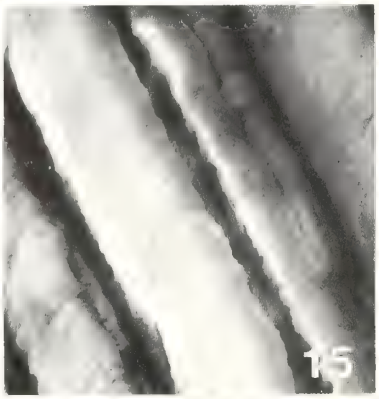
Fig. 1. Byssus of *Anomia simplex*. Uppermost lamellated portion is ventral and basal expanded plaque is dorsal. Horizontal field width = 5.9 mm. **Fig. 2.** Oblique side view of byssus. Lamellae of byssus are readily apparent from this angle. Horizontal field width = 8.5 mm. **Fig. 3.** Light micrograph of byssal notch and right valve. Horizontal field width = 34.0 mm. **Fig. 4.** Ventral view of byssus. Horizontal field width = 2.8 mm. **Fig. 5.** View of dorsally oriented lamellated byssal surface. Horizontal field width = 3.8 mm. **Fig. 6.** Region of byssus showing tapering lamellae as they approach basal plaque. Horizontal field width = 740 μm. **Fig. 7.** Basal plaque at low magnification revealing fine granular surface. This portion of basal plaque in life is covered by flap-like tongue of byssal gland. Horizontal field width = 1.2 mm. **Fig. 8.** Attachment zone of basal plaque and substratum. Basal plaque is pitted with numerous pores in this region. Horizontal field width = 560 μm. **Fig. 9.** Periphery of basal plaque at level of attachment shows irregular outline of active growth zone. Calcareous deposits along the growth zone appear to be laid down on an organic sheet (s). Horizontal field width = 460 μm. **Fig. 10.** Closer view of growth zone on basal plaque reveals an apparently organic substance (0) leading a granular calcified zone (G). Horizontal field width = 135 μm.

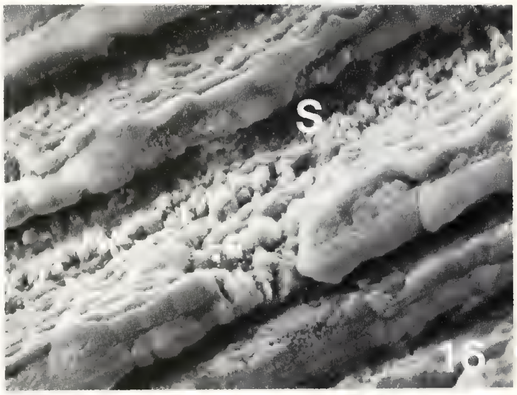


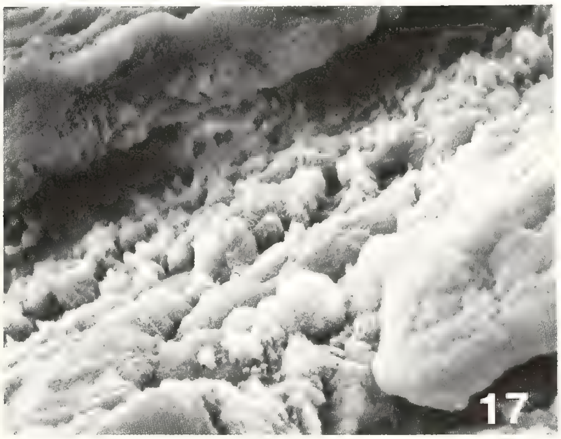


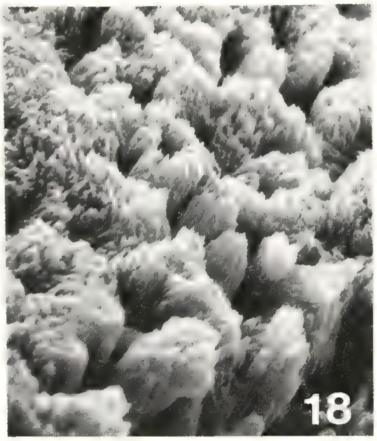












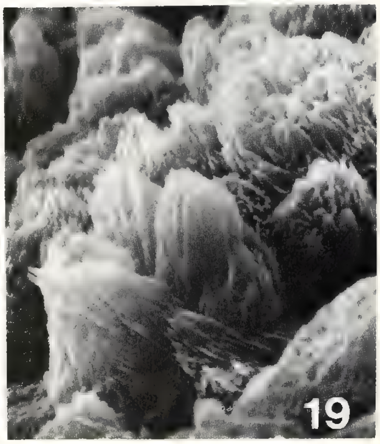
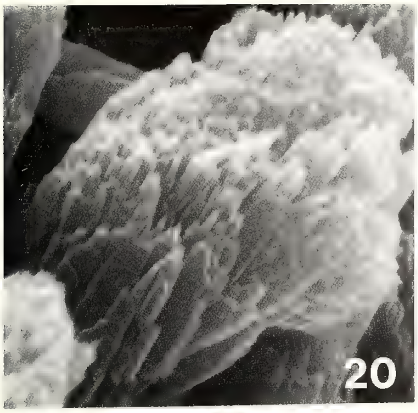
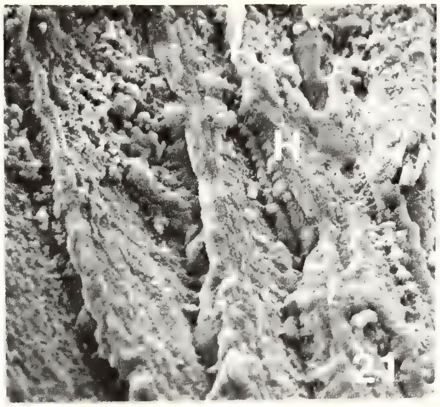
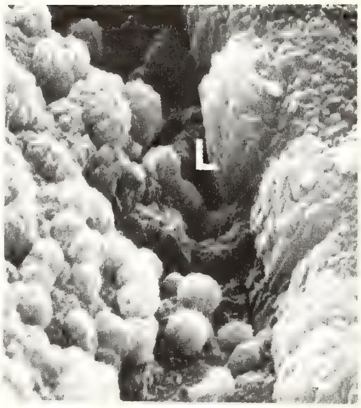
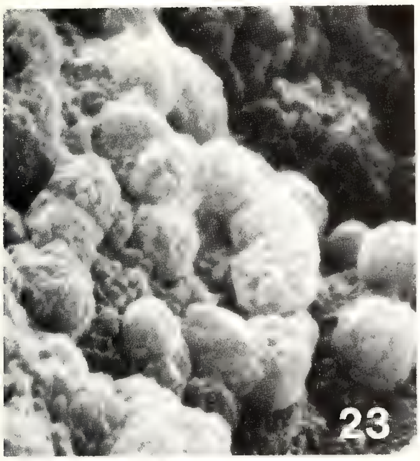


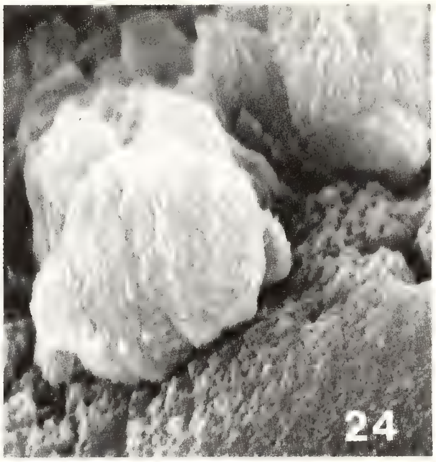
Fig. 11. Ventral surface of byssus reveals irregular surface with numerous spindle shaped granules. Horizontal field width = 40 μm. **Fig. 12.** Outer, ventral tip of byssus occurs as a series of parallel ridges. Beneath these ridges ventrally is a hint of superficial ridges confluent with the lamellae. Horizontal field width = 530 μm. **Fig. 13.** Closer view of ventral tip ridges showing superficially smooth surface of ridges and granular appearance of lower older portions. Horizontal field width = 315 μm. **Fig. 14.** Dorsal lamellae showing highly granular appearance. Horizontal field width = 125 μm. **Fig. 15.** Dorsal lamellae showing very smooth surface. Horizontal field width = 195 μm. **Fig. 16.** Lamellae showing smooth outer surface with spindloid granules (S) in grooves. Horizontal field width = 165 μm. **Fig. 17.** Closer view of spindloid granules in lamellar grooves. Horizontal field width = 85 μm. **Fig. 18.** Spindloid granules occur normal to face of lamellae on dorsal surface. Horizontal field width = 30 μm. **Fig. 19.** Spindloid granules composed of a series of microlathes oriented normal to lamellar surface. Horizontal field width = 12 μm.

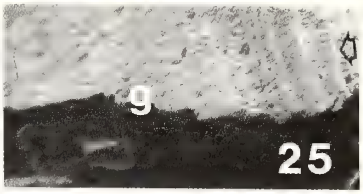


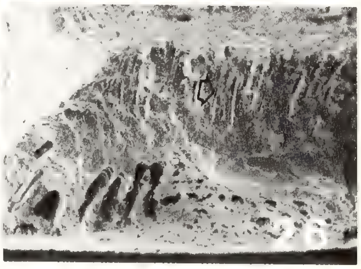


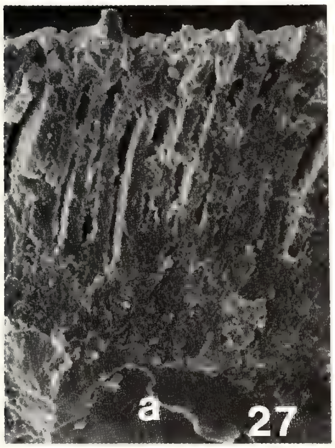


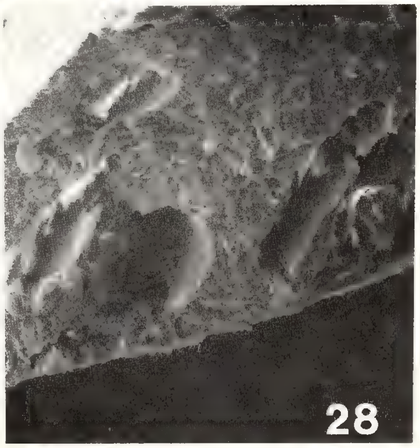












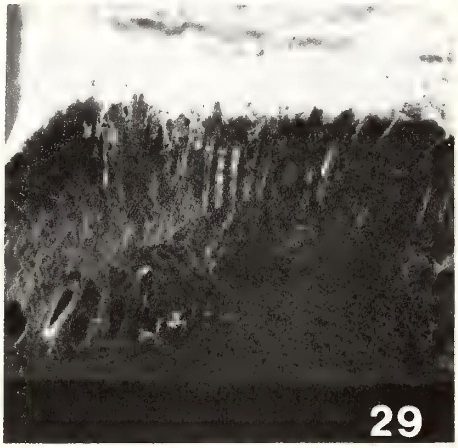


Fig. 20. Closer view of spindloid granule lathes. Horizontal field width = 7.5 µm. **Fig. 21.** Lamellae near point of fusion with basal plaque. Both spindle shaped granules and small hillocks (H) occur here. Horizontal field width = 175 µm. **Fig. 22.** Closer view of hillocks in lamellar grooves. Note lathe-like consistency of portions of lamellar wall (L). Horizontal field width = 8.5 µm. **Fig. 23.** Detailed view of hillocks revealing polygonal subunits. Horizontal field width = 4.5 µm. **Fig. 24.** At higher magnification the compact substructure of the lamellar hillocks is evident. Horizontal field width = 7.0 µm. **Fig. 25.** Cross-sectional fracture of byssus revealing outer fine granular layering (g) with indications of substructural microlathes (open arrow). Horizontal field width = 530 µm. **Fig. 26.** Cross-section through byssus showing submergence of lamellae (arrow) and irregular structural design of internal byssus. Horizontal field width = 1.5 µm. **Fig. 27.** Closer view of submerged lamellar structure and smooth internal region (a). Horizontal field width = 365 µm. **Fig. 28.** Oblique view of fracture zone in byssus showing some relatively large pores and canals. Horizontal field width = 440 µm. **Fig. 29.** Irregular internal structure of byssus revealed in cross sectional fracture. Horizontal field width = 1.1 mm.

lamellae continue around to the dorsum as a system of closely packed folds that show a superficially granular structure in some (Fig. 14), while in others gives an extremely smooth appearance (Fig. 15). In the former, the granular appearance may be spread over the entire structure (Fig. 14) or may be confined to grooves (Fig. 16). In either case a closer look at the granulation reveals that it is caused by spindle-shaped crystals similar to those found on the ventral byssal surface (Figs. 17, 18). The spindles in this case are aligned perpendicular to the lamellar face and average just under 6 μm in length. At higher magnifications the substructure of the spindles is revealed as a series of small lath-like subunits aligned in the direction of the long axis of the spindle (Figs. 19, 20).

As lamellae are followed basally they shorten and there is a distinct change in structure. Near the zone of merger between lamellae and the basal plaque region, lamellar grooves are covered not only by spindle-shaped structures, but often by small hillocks (Figs. 21, 22, 23) composed of irregular polygonal subunits (Figs. 23, 24). Often one side of the groove is dominated by spindle-like substructures and the other by small hillocks (Fig. 21). The underlying surface of lamellae often shows through as being relatively smooth and composed of a very fine grained structure (Fig. 24) or microlaths (Fig. 22).

Cross-sectional fractures through the byssus reveals the sometimes superficial nature of the outer calcareous granular coat (Fig. 25). The thin, outer irregular layer covers a more homogeneous internal structure (Fig. 27). Remnants of lamellae, not yet totally fused into the internal structure, are often evident (Figs. 26, 27). In heavily etched specimens (i.e. prolonged treatment with sodium hypochlorite), deep interlamellar grooves are usually apparent, revealing the organic nature of the interlamellar regions once occupied by byssal gland tissue and byssal gland organic secretions.

In some fractured byssi large pores are obvious, especially along the posterior long axis (Figs. 26, 28). These might be of an extraneous biogenic nature but this is uncertain at this time. Between these pores and buried lamellae, the internal structure of the byssus is finely granular, irregulary lathed and sometimes extremely smooth (Fig. 29).

Under the dissecting microscope fractures also reveal the lamellar nature of the byssus. When stained with toluidine blue, fractured specimens reveal a linear network of parallel lines that stain beta metachromatically indicating an organic substance between calcified lamellae.

Byssus mineralogy

The Feigl stain gave variable surficial results with different byssi. In some it showed a totally blackened outer structure that may indicate all aragonite. In others only the dorsal outer surface stained (Fig. 30), while in still others an irregular superficial mosaic stain was achieved. Fracture cross-sections of the byssus showed only superficial positive Feigl staining and not in all byssi tested. The internal byssal core never gave a positive (black) aragonite stain reaction. Because of the fine, irregular surface of the spindles, which may cause false staining, the Feigl test was backed up by X-ray diffraction. X-ray diffraction left no doubt that both aragonite and calcite were often present in the byssus. Small size demanded the use of several byssi in a single diffraction analysis, so a mixture of 2–4 specimens were tested at any one time. Each case resulted in readings that indicated the presence of both mineral types. Diffraction analysis of even mixed byssi samples always showed a qualitatively greater proportion of calcite than aragonitic.

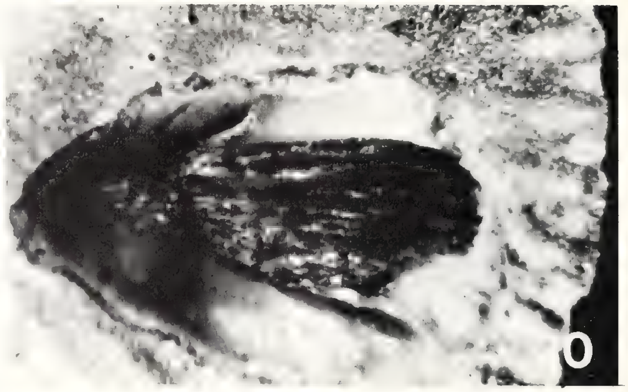


Fig. 30. Light micrograph of byssus stained with Feigle solution. Horizontal field width = 6.5 mm.

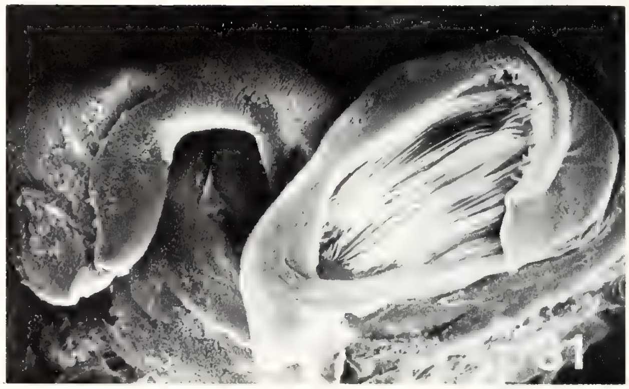


Fig. 31. Critical point dried foot and byssal complex. Spatulate foot occurs on the left of the cup-shaped, lamellate byssal gland. Horizontal field width = 8.2 mm.

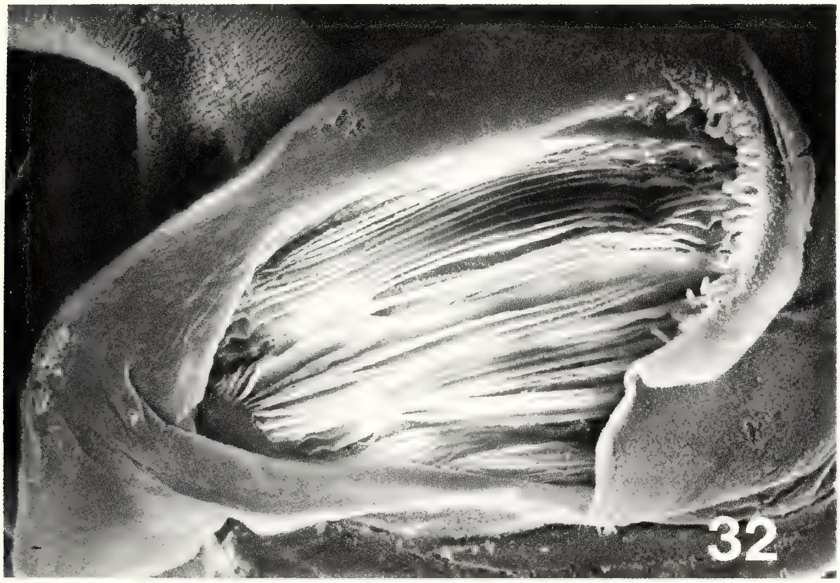
Byssal gland and foot structure

The foot of *Anomia simplex* is reduced to a small vermiform structure with an enlarged flexible, bulbous to flat tip (Fig. 31). The tip of the foot can inflate and contract into a variety of shapes and sizes. This pedal region is dense with mucocytes and likely functions to keep the byssal notch area free of debris. The tip of the foot when relaxed, very closely approximates the diameter of the byssal shell notch. Although with the byssus present the foot cannot penetrate the notch, the foot is able to flatten out into a spatulate form and possibly clean the peripheral crevices around the aperture.

At the base of the foot is an expanded, cup-like structure that composes the byssal lamellar gland (Figs. 31, 32). This cup-like region is formed of numerous fine tissue folds. Each pair of byssal gland folds border a single calcified byssal lamella. In adult individuals, there are between 30–45 calcified lamellae. The central lamellated or folded region of the gland is surrounded by a thin extension of the periphery of the byssal gland cup. The latter cradles the exterior of the byssus within the bivalve (i.e. interior to the byssal notch). Elongated finger-like projections are present on the fused, ventral side of the byssal gland cup (Fig. 32), and a tongue-like flap is located dorsally and covers the basal flare of the byssus (Fig. 33). The digitate extensions border the apical lamellae near the outermost portion of the byssus ventrum.

Histological sections reveal the very thin structure of individual gland folds (Fig. 34). Folds are extensions of the byssal-pedal musculature and muscle fibers frequently extend into the tissue folds (Fig. 35). This arrangement may account for the firm connection between byssal gland and byssus. Muscle tension may narrow gaps between adjacent gland folds and place pressure on the calcified byssal lamellae.

Periodically in histological section, organic fibers or ribbons occur between the gland folds (Fig. 36; O). These organic secretions produce a beta metachromatic stain with toluidine blue.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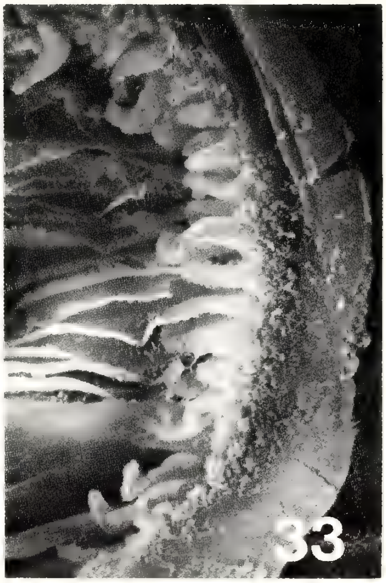
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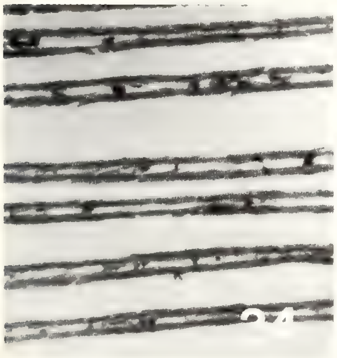
Fig. 32. Closer view of byssal gland showing numerous fine folds composing secretory surface of byssal calcified lamellae. Horizontal field width = 5.4 mm. **Fig. 33.** Finger-like projection of ventral portion of byssal gland cup. Horizontal field width = 0.8 mm.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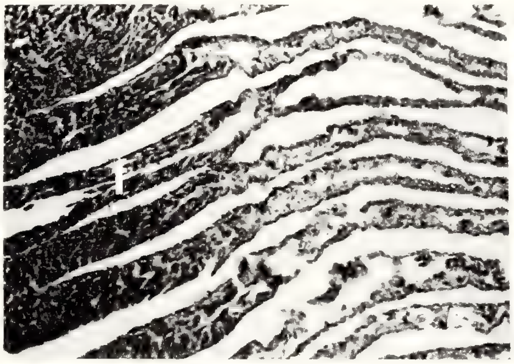

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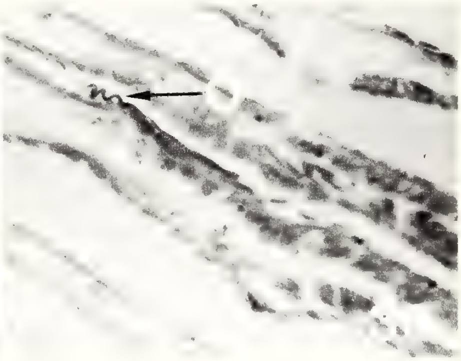

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Fig. 34. Histological section through folds of byssal gland. Modified Pantin. Horizontal field width = 340 μm. **Fig. 35.** Histological section through byssal gland showing infiltration of muscle fibers (f) within gland folds. Modified Pantin. Horizontal field width = 510 μm. **Fig. 36.** Histological preparation showing organic ribbons (0) between folds of byssal gland. Toluidine blue. Horizontal field width = 185 μm.

DISCUSSION

Highly folded byssal glands in a cup-like retainer have also been found in some scallops (Gruffydd, 1978) but in these the gland produces a series of flattened ribbons of a protein or mucopolysaccharide nature. In *Amonia simplex* the gland produces a calcified byssus composed of two basic microstructural and often mineralogical forms.

Contrary to initial hypotheses, the byssal gland produces a basically calcitic byssus column. Based on histological sections it appears that each calcified lamella may have an organic core or matrix. Gland lamellae often show an organic ribbon-like secretion between adjacent folds (i.e. site of calcified lamellae secretion). Following treatment of the byssus with an organic solvent *in vitro,* "dissolved" interlamellar regions are evident in areas apparently beneath the reach of byssal gland tissue. Deposition of the basal (i.e. plaque) calcite also appears to be dependent upon initial production of an organic sheet. Presence of an organic matrix or nucleation layer may regulate calcification (Degens, 1965). Hare (1963) suggests that certain side chains, possibly acid mucopolysaccharides bound to proteins by specific amino acid side chains (Wada, 1964a, b), may concentrate and localize calcium and carbonate ions and provide the impetus for calcification and nucleation. Wada and Furuhashi (1971) suggest that sulfated acid mucopolysaccharides act as calcium carriers providing calcium concentrations high enough to initiate mineralization. Wheeler et al. (1981), however, have found a protein in the soluble organic shell matrix of *Crassostrea virginica* that binds calcium and suppresses calcium carbonate nucleation and crystal growth.

The possibility that composition of the organic matrix controls mineralogy has been examined by many authors (Beedham, 1958; Watabe and Wilbur, 1960; Simkiss, 1965; Wilbur, 1964; Grégoire and Lorent, 1972; Weiner and Hood, 1975; Nakahara et al., 1980). Many organisms with calcium carbonate skeletons have crystals closely associated with an organic matrix (Watabe, 1974) that may serve as a crystal nucleation site (Watabe, 1981). This being the case, the matrix may exert a primary influence on mineralogy. Distinct chemical differences have been found in the matrix of calcitic and aragonitic shell layers.Different amino acids, for example, have been reported in the organic matrices of the two primary biological calcium carbonate morphs (calcite and aragonite) by Roche et al. (1951), Tanaka et al. (1960), and Hare (1963). Differences in amino acid composition, however, may not readily explain "mineral selection" since Travis et al. (1967) discovered variations in amino acid composition in different layers of monomineralogic shells that vary as much as or more than the differences seen in adjacent layers of bimineralogic shells. Insoluble and soluble portions of the molluscan organic matrix are usually present. These components, varying in composition, may be found in different places within the shell matrix milieu. Krampitz et al. (1976) identified calcium ligands in the water-soluble matrix of some gastropods. This ligand may stimulate mineralization. The soluble fraction of the matrix, proportionally less abundant than the insoluble fraction, may be confined within crystals or in or on the insoluble, interlamellar matrix (for review see Watabe, 1981).

Further evidence of the role that organic layers or matrices may play in control of calcium carbonate deposition and mineralogy resides in potential influence of periostracum. In molluscs with well developed bimineralogic (aragonite and calcite) shells, initial calcification may occur on the periostracum and was thought to be calcite (Kennedy et al., 1969). Carriker (1979), however, described the mosaicostracum of *Mytilus edulis* and suggested that this "attachment" layer was aragonitic. Kennedy et al. (1969) claim that "The role of periostracum and/or organic matrix in initiating calcification, and thus controlling the deposition of either aragonite or calcite, cannot be doubted. . . ." During shell regeneration, some molluscs may first form a thin, organic sheet, similar to periostracum, before initiating calcification (Kawaguti and Ikemoto, 1962).

The thin organic ribbons often seen between byssal gland folds in *A. simplex* may be precursors of calcification of the byssal lamellae. Organic byssal threads of *Chlamys islandica* are produced by a similar byssal gland (Gruffydd, 1978). Here glycine composes 11.0–15.5% of the byssal amino acids (Gruffydd, 1978). Glycine is also not an uncommon amino acid in the decalcified byssus of *A. simplex* (J. H. Waite; personal communication, 1983).

The step between producing proteinaceous byssal threads and altering the chemistry of those threads sufficiently to initiate calcification may not have been a "complex" evolutionary change. Organic byssal ribbons of *A. simplex* probably function as might the organic templates described earlier. The organic sheet laid down in front of the calcified basal byssal plaque also indicates the possible role in nucleation played by organic structures during and preceding calcification. Organic ribbons or sheets act as nucleation sites that may favor the production of calcite. Since very thick oyster shells are mainly calcitic, seawater is saturated with calcite, and calcite is the least soluble and most stable of the biogenic calcium carbonate morphs, it might be predicted that crystallization of this mineral type is a simple process (Simkiss, 1965). This is not the case. Calcium carbonate crystals are not easily precipitated from natural seawater and when it does precipitate, it is usually in the form of aragonite (Gee et al., 1937). Naturally occurring orthophosphates and other phosphatic compounds in seawater seem to interfere with calcite precipitation (Simkiss, 1965). Several naturally occurring marine cations (i.e. Mg, Mn, Cu, Zn) also seem to inhibit calcite precipitation (Milliman, 1974).

Outer granular or spindle shaped byssal deposits are likely of inorganic origin. They do not appear in all specimens examined, are aragonite (based on x-ray diffraction patterns and Feigl stain indications) and do not appear uniformly over the entire lamellar surface of the byssus. Aragonite is, as mentioned, preferentially precipitated from seawater. Spindle shaped granules on the surface of the byssus of *Anomia simplex* are also similar to crystals of high magnesium calcite that have been precipitated in the laboratory by Towe and

Malone (1970). Structurally-similar types of crystals have also been found in spine diaphragms of an archaeogastropod (Wind and Wise, 1976), the lithodesma of the anomalodesmacean bivalve *Lysonia floridana* (Prezant, unpublished data), and in regenerating shell of various species of *Tegula* (Reed-Miller, 1983 and personel communication). All of these spindloid structures might be of inorganic origin. In many Myoida, however, similar spindles occur in spaces beneath the periostracum (Carter, personel communication, 1983). These may be biogenic in origin. Inorganic precipitation of aragonite, however, on the byssal calcite base may reflect the presence of calcium that has undergone dissolution elsewhere in the byssus (Prezant, 1982). In *Tegula*, Reed-Miller (1982) suggests that areas of shell dissolution may be responsible for the aragonitic, spindloid deposits in regenerating shell. The inconsistent presence of aragonite spindles on the byssus may indicate a temporal event occurring only under appropriate micro-environmental circumstances. At present we have little understanding of what these circumstances might be although it is likely that the spindles are deposited only while the byssal gland is inactive. Thus, in *A. simplex,* when the byssal gland is not producing the calcitic byssal core, residual Ca^{2+} and CO^{2-}_{3} ions may inorganically precipitate out onto the calcite lamellar base as aragonitic spindles. Macroenvironmental regimes are known to influence mineralogies of molluscan and other phyla shells (see review in Carter, 1980). It is reasonable to assume microenvironment is the final coordinator of mineralization.

The overall byssus-byssal gland system of *Anomia simplex* presents a structure well adapted to this bivalve's sessile lifestyle. The small, flexible vermiform foot likely functions to keep the peripherally exposed byssal notch area clean. The firm connection between gland and byssus is retained by the muscular extensions that run into the gland folds. Contraction of these muscle fibers will place pressure on the calcified byssal lamellae and help maintain a firm connection in the living animal. The expanded byssal plaque with an underlying organic layer, offers an expanded flattened surface for attachment to the substratum. Actual basal attachment to the substratum is probably not a structural feature of the calcified byssus but may be a chemical bond involving an organic basal portion that precedes and underlies the calcified byssal plaque. Waite (1982) and Waite and Tanzer (1981) have recently described a bonding protein system for the byssal plaque of *Mytilus edulis*.

The advantages of a calcitic (versus aragonitic) primary byssal column is uncertain. Calcite structures are generally less dense than aragonite structures (Carter, 1980). Carter (1980) suggests that a low density, porous structure in some sedentary bivalves may be associated with "crack-stopping mechanisms, economy of secretion, or rapidity of shell layer thickness increase." The byssus is the sole adhering structure that allows retention of *Anomia* on some substratum. The porous basal portion of the calcite basis of *A. simplex* is well suited for this arduous task and well adapted for fracture resistance and, perhaps, rapidity or economy of secretion.

The soft dorsal tongue-like flap of the byssal gland may be responsible for the contoured, nonlamellate basal surface of the dorsally directed byssal attachment plaque. This area is either never lamellate and the flap may be directly responsible for its production or is secondarily involved in fusion of lamellae. The subtle change from lamellae to plaque supports the latter conjecture.

Small finger-like projections along the dorsal right edge of the byssal gland may mold or contour calcareous byssal secretions as they are deposited upon an organic substrate.

Many questions concerning this system remain. The exact mode of lamellar secretion is unknown. The qualities of the organic ribbons that apparently precede calcification are unknown. The adhesive nature of the basal plaque undersurface remains to be explored as does the possible adaptive features of aragonitic surface granules. Might the aragonitic surface be deposited regularly between periods of primary calcite deposition? Since this type of inorganic precipitation of calcium carbonate is not unique to *Anomia simplex*, how common is it? It is certain that a closer look at biogenic versus nonbiogenic calcification in molluscan systems is called for.

ACKNOWLEDGMENTS

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STATOLITH DEVELOPMENT IN THE OMMASTREPHID SQUID *ILLEX ILLECEBROSUS* (LESUEUR, 1821)

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ABSTRACT

Squid of the ommastrephid species *Illex illecebrosus* were collected off Newfoundland, ranging in dorsal mantle length of 13.5–271 mm. Developmental stages of statoliths over this size range are named, described and illustrated. The Juvenile Stage in this series is coincident with the initial development of most adult morphological features.

Statocysts are organs of equilibrium detection found in many motile invertebrates. In cephalopods, they are paired, complex, saccular organs located ventrally within the posterior cephalic cartilage and serve to detect linear and angular accelerations (Figs. 1 and 2.)

Although statolith form varies considerably among teuthoids, several features are common to nearly all. Teuthoid and sepioid statoliths are composed of aragonite (Clarke, 1978), in a thin matrix of protein (Radtke, 1981). Clarke (1978) devised a standard nomenclature for these structures and a system of measurements. Since teuthoid statoliths are apparently species-characteristic and have a greater likelihood of fossilization than other structures, they have potential for identification of fossil species (Clarke and Fitch, 1975). The metrical and nominal descriptive system has been used to identify several new fossil species based on single statoliths (Clarke and Fitch, 1979), recognizing, however, intraspecific variation. Such variation has been demonstrated in *Symplectoteuthis oualaniensis* (Lesson) by Burch (1980), and considerable intraspecific and intra-individual variation has been shown in *Illex illecebrosus* by Morris (1980, 1981). Thus, some doubt may be cast on the validity of descriptions based solely on one statolith from a specimen.

Statolith crystals are in two distinctly different arrangements (Dilly, 1976; Morris, 1980). The first is an irregular arrangement found in the wing, the ventral portion of the dorsal spur, and the medial portion of the rostrum (Fig. 3). These areas appear opaque under a light microscope (Morris, 1980). The second pattern involves nearly parallel orientation of the long axes of the crystals radiating from the nucleus and is found in the dorsal and lateral domes, most of the rostrum and in the central region. These regions are

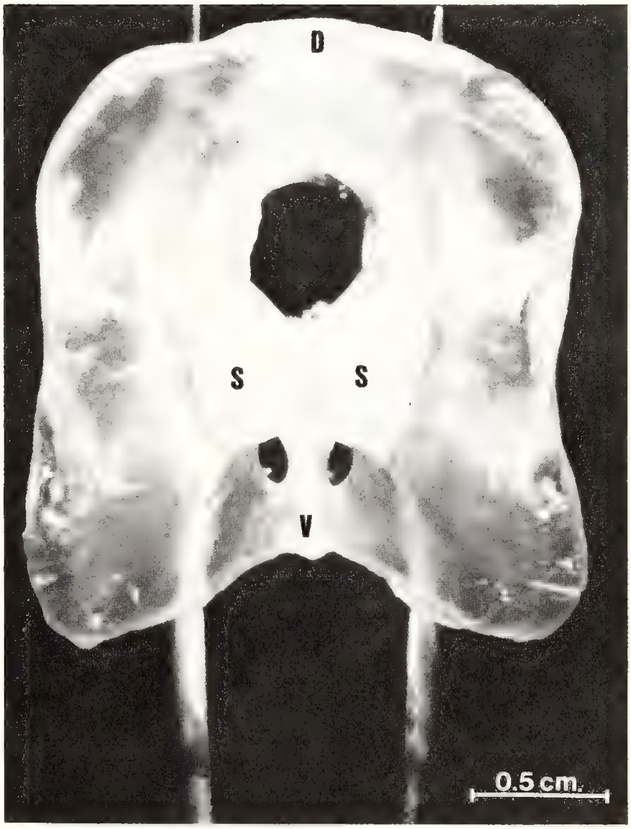

Fig. 1. Photograph showing posterior view of the cephalic cartilage of *Illex illecebrosus* (Lesueur) illustrating the location of the statocysts. (From Morris, 1981). D, dorsal; S, location of statocysts; V, ventral.

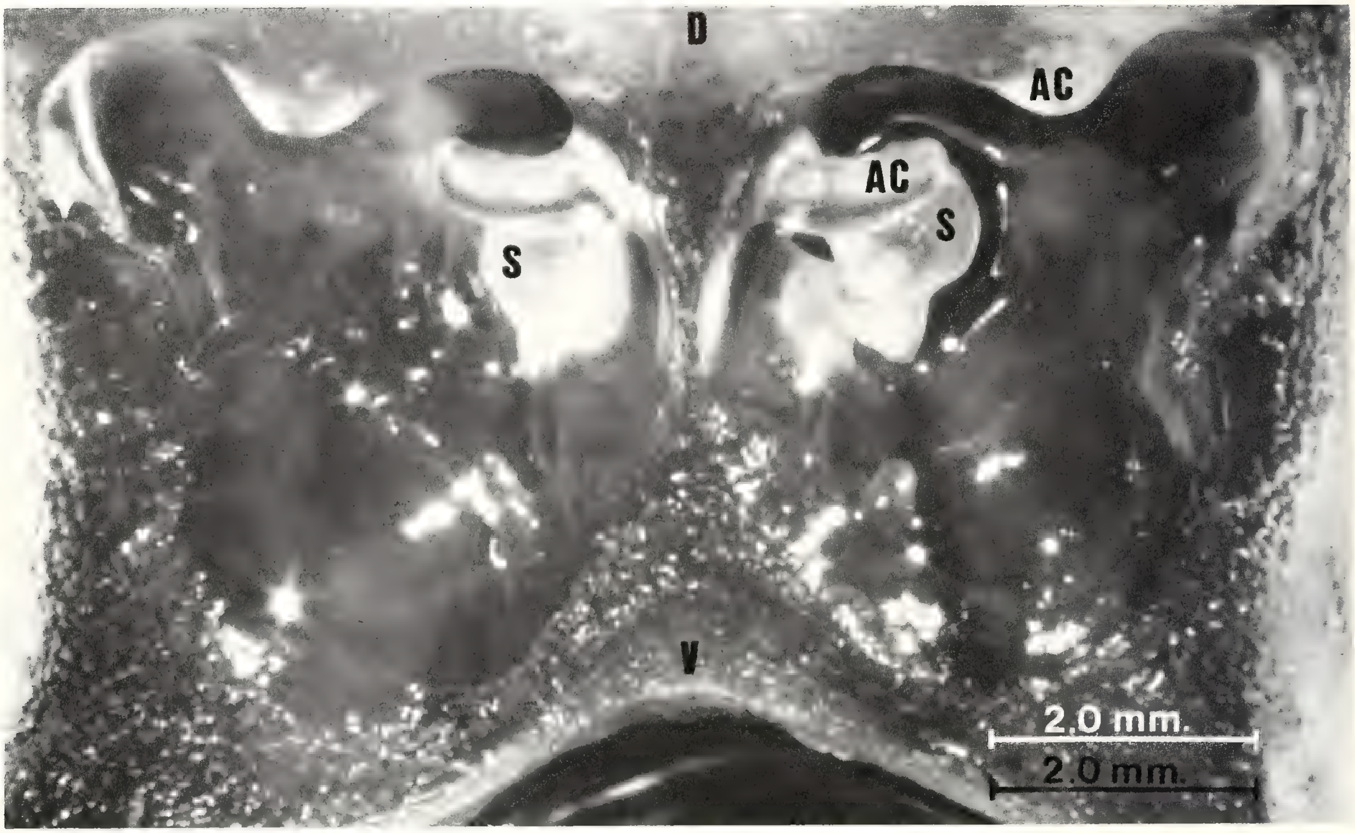

Fig. 2. Photograph of a vertical section through the statocysts of *Illex illecebrosus* (Lesueur) showing the anterior region of the statocysts and the statoliths *in situ*. (From Morris, 1980). AC, anticrista; D, dorsal, ST, statolith; V, ventral.

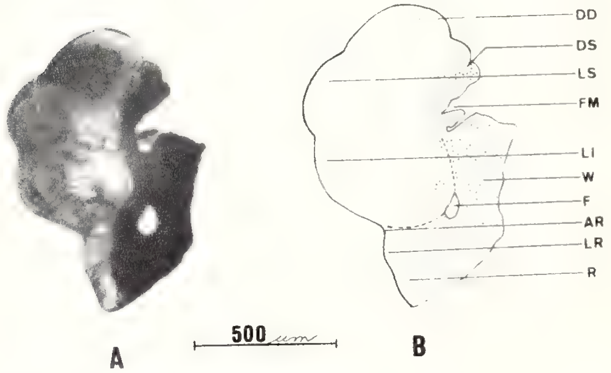

Fig. 3. Posterior aspect of the statolith of *Illex illecebrosus* (Lesueur) showing visible structures referred to in this study. A. Light Micrograph. Notice opaque region composed of irregularly arranged crystals toward medial side of statolith. B. Diagram. Dotted line indicates position of posterior dome indentation. Stippled area indicates region of irregularly arranged crystals. AR, rostral angle; DD, dorsal dome; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; LR, lateral lobe of rostrum; LS, superior lobe of rostrum; R, rostrum; DS, dorsal spur; W, wing. (Modified from Morris, 1980: Nomenclature as from Clarke, 1978.)

translucent (Morris, 1980). Growth increments may be visible in these latter areas in unground specimens.

The stages in structural development of a cephalopod statolith are described here for the first time. Lipinski (1980) presented photographs of statoliths of *I. illecebrosus* that show development, but failed to identify developing structures, thus neglecting to trace their developmental anatomy into adulthood.

MATERIALS AND METHODS

Specimens of *I. illecebrosus* were captured on five occasions during 1981 (Table 1 and Fig. 4) and were frozen in sea water until examination.

Statolith removal was performed by placing the squid on its dorsum, lifting the hyponome, and severing the tissues attaching the latter to the head. A vertical incision anterior to the hepatic portion of the digestive gland to the depth of the esophagus exposed the broad posterior cephalic cartilage. Removal of the tissues surrounding this cartilage exposed the two convex cartilaginous protuberances that cover the statocysts. The statoliths were usually visible through the cartilage. A horizontal incision through the posterior cephalic cartilage exposed the statoliths, which were then separated from their maculae and stored in glycerine. Following removal of excess tissue and washing in distilled water, statoliths were photographed in glycerine.

RESULTS

General

In the two earliest samples (February and March, 1981), which contained the smallest specimens (Table 1), the squid exhibited several larval characteristics including a loose saccular mantle, wide proximal aperture of the hyponome, proportionately large eyes relative to the adult, and a posteriorly convex fin. Statoliths were easily removed from even the smallest specimen (13.5 mm DML).

Specimens taken in June were still relatively small, (Table 1), but were similar morphologically to adults captured in October.

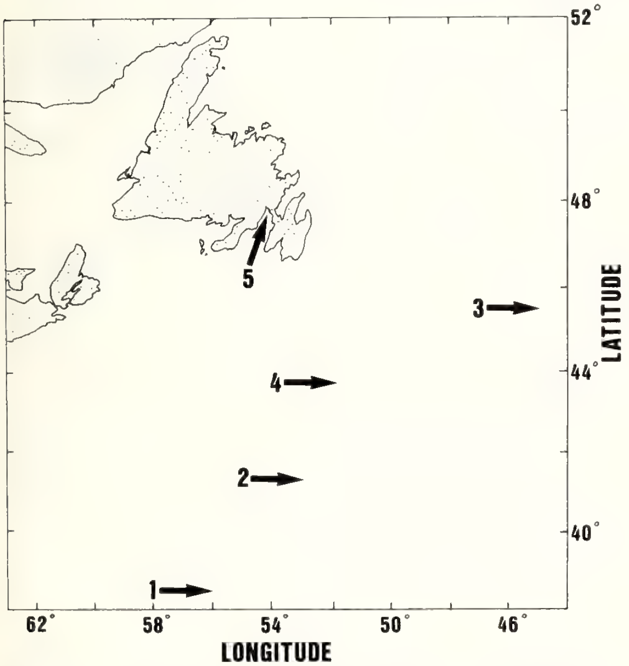

Fig. 4. Map of Northern Gulf Stream region and insular waters of Newfoundland, showing sources of *Illex illecebrosus* (Lesueur). (See Table 1).

Statolith Development

As larger specimens with larger statoliths were taken at progressively later dates, the statolith became increasingly complex and passed through several distinct stages. These stages are described below.

Primordial Stage: The developmental stage that follows nucleus formation has a roughly tear-drop or lachrymiform shape with the tip directed ventrally and flexed slightly anteriorly and laterally (Fig. 5). The Primordial Stage is found in specimens smaller than 14 mm DML. The dorsal region of this structure, the dome anlage, is the precursor of the dorsal dome and superior lateral dome. The medial curvature, after enlarging as the statolith grows, will form the attachment site for the wing. The rostrum anlage is the apex of the lachrymiform structure.

Definitive Stage: The second stage in post-nucleus statolith development, the Definitive Stage, occurs in squid of approximately 30 mm DML (Fig. 6). The dorsal dome, superior lateral dome and inferior lateral dome are forming and easily identifiable. The rostrum is recognizable and is altering its direction of growth, curving toward the midline of the cephalic cartilage *in situ*. The medial aspect of the rostrum bears small irregularly arranged crystals that form the anlage of the wing. Irregular crystals that effectively obscure the underlying increment lines have begun to form in the dorsal region. The dorsal spur begins to form in the dorso-medial region.

Table 1. Dates of capture and sizes of *I. illecebrosus* taken at five sites for statolith analysis, 1981.

Site of capture	Date	No.	Location	Range DML (mm)	Range statolith length (μm)
1.	Feb. 27, 1981	10	38° 24.7′ N 56° 00.0′ W	13.5–29.0	281–442
2.	Mar. 4, 1981	3	41° 14.9′ N 53° 00.0′ W	21–30	366–397
3.	May 25, 1981	5	45° 00.1′ N 45° 30.0′ W	109–118	772–818
4.	June 20, 1981	49	47° 45.1′ N 54° 0.1.2′ W	157–191	851–945
5.	Oct. 15, 1981	48	47° 45.1′ N 54° 01.2′ W	229–271	1033–1139

DML = dorsal mantle length. (See Figure 4)

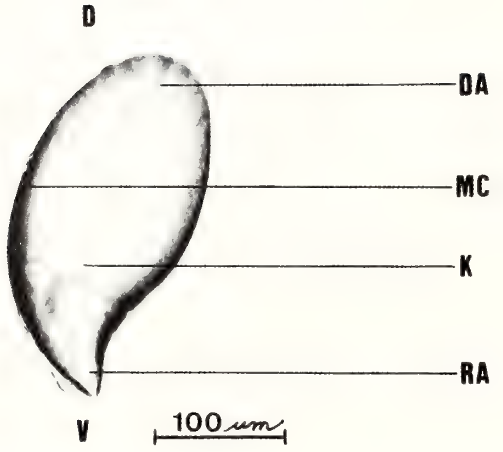

Fig. 5. Primordial Stage in the development of a left statolith of *Illex illecebrosus* (Lesueur) from an unsexed specimen of 13.5 mm dorsal mantle length. (Anterior view). D, dorsal; DA, dome anlage; K, kernel; MC, medial curvature; RA, rostrum anlage; V, ventral.

Pre-Juvenile Stage (Hypothetical): The third stage, the Pre-Juvenile Stage, is not illustrated because of lack of specimens. Several of its characteristics, however, may be inferred. For the sake of continuity we speculate on its appearance and role in the developmental series. The rostrum extends ventrally, and medially. The wing extends medially, then turns anteriorly toward the medial curvature. The dorsal spur is distinct as are the dorsal and lateral domes. Obscuring crystals continue to be laid down on the anterior surface.

Juvenile Stage: In the Juvenile Stage the wing extends upward and connects to the medial curvature, thereby completing a surface that bears a foramen through the statolith (Fig. 7). Further extension of the wing results in the creation of the medial fissure, a discontinuity between the wing ventrally and the dorsal spur dorsally. Obscuring crystals continue to form. This stage is found in specimens of 109 to 118 mm DML.

Adult Stage: The Adult Stage is found in late juveniles and sexually maturing or mature adults (DML over 118 mm). In the adult statolith, the inferior lateral dome may be subdivided so that the entire lateral dome is tripartite (Fig. 8). The foramen gradually becomes filled by the deposition of

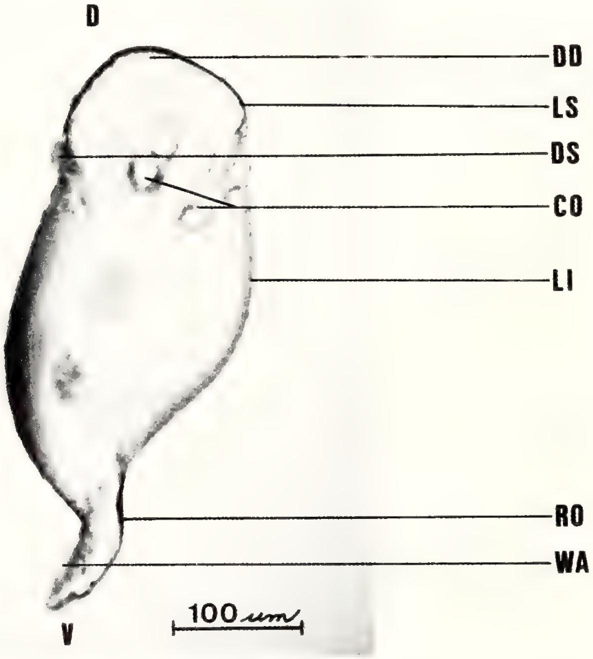

Fig. 6. Definitive Stage in the development of a left statolith of *Illex illecebrosus* (Lesueur) from an unsexed specimen of 29.0 mm dorsal mantle length. (Anterior View). CO, occulting crystals; D, dorsal; DD, dorsal dome; DS, dorsal spur; LI, inferior lateral dome; RO, rostrum; V, ventral; WA, wing anlage.

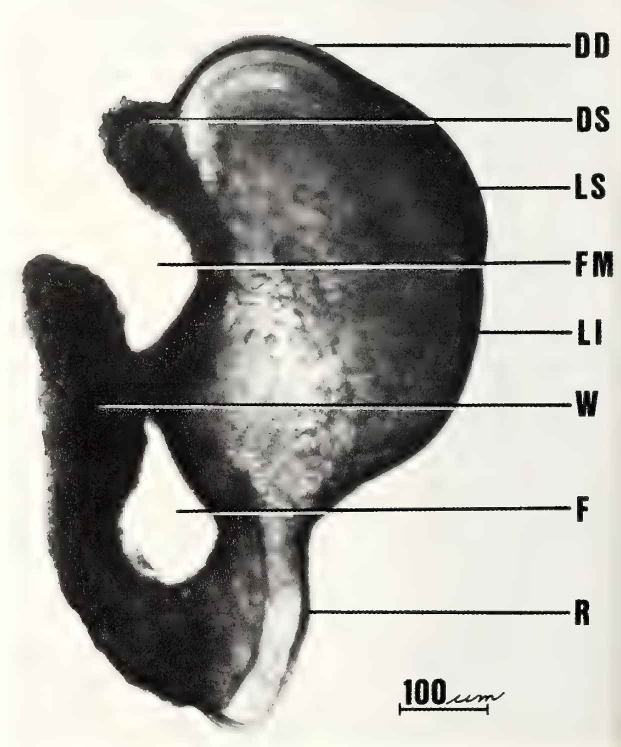

Fig. 7. Juvenile Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a female specimen of 109 mm dorsal mantle length. (Anterior view). DD, dorsal dome; DS, dorsal spur; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; SS, superior lobe of lateral dome; R, rostrum; W, wing.

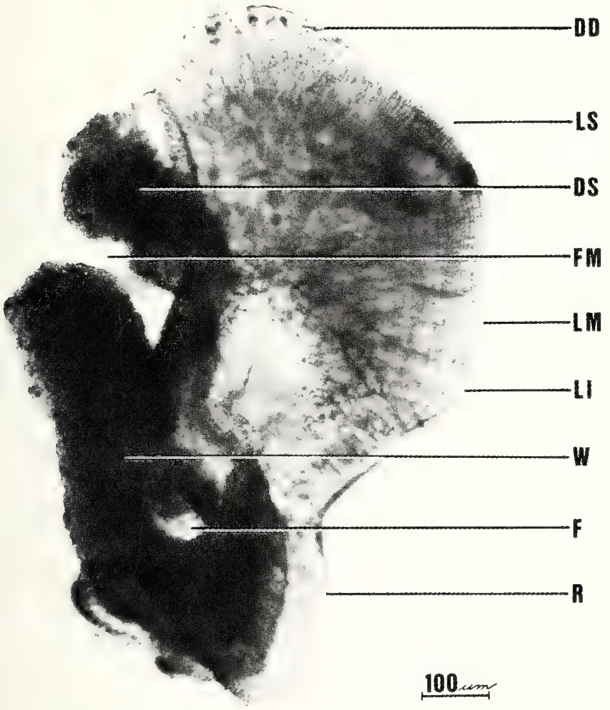

Fig. 8. Adult Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a female specimen of 244 mm dorsal mantle length. (Anterior view). DD, dorsal dome; DS, dorsal spur; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; LM, medial lobe of lateral dome; LS, superior lobe of lateral dome; R, rostrum; W, wing.

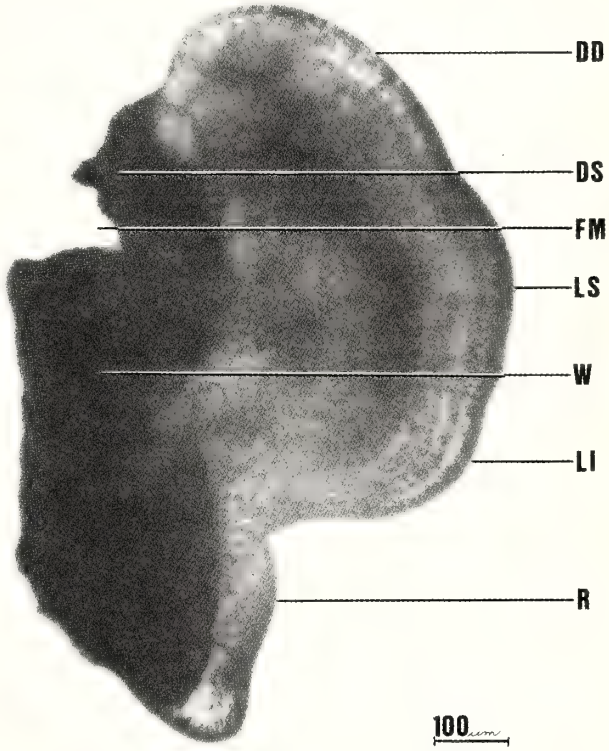

Fig. 9. Advanced Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a mature male specimen of DML 230 mm. (Anterior view). DD, dorsal dome; FM, medial fissure; LI, inferior lobe of lateral dome; LS, superior lobe of lateral dome; R, rostrum; DS, dorsal spur; W, wing.

crystals and the medial fissure similarly narrows. Irregular obscuring crystals cover most of the anterior surface of the statolith in this stage, with the exception of the immediate area of the nucleus. It should be noted that these crystals are heavily concentrated in the region of their genesis, indicating their continual production and deposition in that area. The area of their deposition, however, expands with age and time.

Advanced Stage: In the Advanced Stage (Fig. 9), the structure of the statolith is similar to that of the Adult Stage except the foramen and medial fissure are closed, having been filled by crystalline deposits. The lateral dome may or may not be tripartite. Right and left statoliths from the same animal have been seen to vary in having the tripartite condition of the lateral dome in one but not in the other. The Advanced Stage appears in squid of minimum DML of 230 mm.

As the growing statolith passes through these stages, changes in the pattern of increment deposition are visible. These patterns are characteristic of different parts of the translucent portion of the statolith (Morris, 1983).

DISCUSSION

The first part of a teuthoid statolith to be formed and subsequently recognized during development is the kernel. The kernel, not to be confused with the nucleus which includes the kernel (Morris, 1983), is a small spheroidal area lying near the wing of the statolith in the adult animal. It is visible in statoliths from very young specimens (Fig. 5) and in ground statoliths from adult specimens. Growth increments in the kernel are absent or indistinct.

The kernel is analogous to the kernel of fish otoliths in representing the formation or growth of the statolith prior to the deposition of clearly recognizable increments. Thus, the statolith exists in the form of a very small kernel before the deposition of the first increments. The nucleus of fish otoliths consists of the kernel plus the first opaque increment (Pannella, 1980). Such a prominent increment can be found around the kernel of statoliths of squid (Figs. 5 and 6), thus distinguishing the kernel from the adjacent extranuclear area.

A basic change in overall shape throughout the developmental sequence is apparent. Early, the basic configuration is lachrymiform (Primordial Stage, Fig. 5) and this shape can be traced by following incremental darkenings around the nucleus (Fig. 6). Soon the lachrymiform shape is altered as the statolith enters the Definitive Stage (Fig. 6) at which time *I. illecebrosus* has attained a dorsal mantle length in excess of 14 mm. The larval stage of the ommastrephid family is classically considered to end with the separation of the proboscis to form the tentacles, thus ending the rhynchoteuthoid stage (Chun, 1915). This occurs at DML of 8.5–9.5 mm (Roper & Lu, 1978, Vecchione, 1978). The statolith development, however, indicates that the larval stage is still present at DML of 14 mm, which suggests that larval biology and morphology extend beyond the rhynchoteuthion.

The anlagen, or precursors, of specific statolith structures so evident in the Adult Stage first arise during the Definitive Stage. The single exception to this is the rostrum anlage, which is first evident in the Primordial Stage. Indeed, the rostrum has assumed a configuration clearly similar to that of the adult as early as the Definitive Stage.

During the Pre-Juvenile stage, the anlagen are developed to such an extent that the statolith is characterized by all the adult structures in their proper adult positions and in approximate adult proportions.

Although there are some morphological changes in statoliths between Juvenile and Adult Stages, most changes are associated with increase in size. As expected, squid with juvenile statoliths have a body morphology which is essentially that of the adult (except for size and sexual organ development). The level of development of body morphology and associated maneuvering ability are apparently reflected in the degree of complexity and developmental stage of the statoliths.

A clear demarcation between Juvenile and Adult statolith forms is not obvious, but the ventral portion of the medial fissure is widely open in the Juvenile Stage and closes in the Adult, and the foramen of the Juvenile shows no crystalline deposits.

The Advanced Stage is very uncommon, having been found in less than 1% of the more than 400 pairs of statoliths of *I. illecebrosus* examined. Although specimens with the foramina filled are often found, an accompanying closure of the medial fissure is atypical, particularly to the extent illustrated in Figure 9. This form, i.e. the Advanced Stage, may be within the range of normal variation expected in the adult configuration, but at present we have no basis for an explanation of this phenomenon. We suggest that it represents the final configuration of the statolith typical of the Ommastrephid after it has left the insular waters of Newfoundland and begins its supposed southerly migration into its oceanic habitat.

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SOME EARLY NAMES IN CANCELLARIIDAE

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ABSTRACT

Gmelin (1791) proposed six species-level names in the family Cancellariidae. Of these, *Buccinum piscatorium* Gmelin is in common usage (as *Cancellaria (Solatia) piscatoria* (Gmelin)); *Murex semilunaris* Gmelin is a junior synonym of *C. piscatoria*; and *Buccinum pyrozonalis* Gmelin is a junior synonym of *Cancellaria cancellata* (Linné, 1767). The remaining three names are identifiable senior synonyms of names proposed later. *Buccinum scalare* Gmelin is a senior subjective synonym of *Trigona pellucida* Perry, 1811 and *Delphinula trigonostoma* Lamarck, 1822, the type species of *Trigonostoma* Blainville, 1827. *Murex scala* Gmelin is a senior subjective synonym of *Trigonaphera withrowi* Petit, 1976 and is now placed in the genus *Scalptia. Voluta nassa* Gmelin is considered a senior subjective synonym of *Cancellaria lamellosa* Hinds, 1843 and is referred to the genus *Scalptia.*

Cantharus triplicatus Röding, 1798 is a junior synonym of *Cancellaria cancellata* (Linné, 1767). All known 18th Century species-level taxa in Cancellariidae are listed.

In the 10th Edition of his *Systema Naturae,* Linné described only one species of the Neogastropod family Cancellariidae. In the 12th Edition another species was added. Prior to the publication of Gmelin's 13th Edition, only four cancellariids had been named. These were the two Linnaean species plus *Admete viridula* (Fabricius, 1780) and *Admetula evulsa* (Solander, 1766). Neither of these latter two names were mentioned by Gmelin. In addition to listing Linné's two species, Gmelin introduced six additional species-level names in the family, although he placed them in three different Linnaean genera. One of these names, *Cancellaria piscatoria* (Gmelin) has been in common usage for many years and is a senior synonym of *Murex semilunaris* Gmelin. Another of his names is a synonym of *C. cancellata* (Linné). The other three Gmelin names have been ignored or mistreated in the subsequent literature. These names have priority over all other names for the species involved if they can be identified; thus, a careful search was made of the literature and the citations and discussions of various authors were studied. It was found that all three of these names can be applied, with varying degrees of certainty, to species which are currently known by later names. By applying the Law of Priority and placing these Gmelin names into general usage, stability will be achieved for these taxa as there is minimal possibility of the existence of senior synonyms.

The opportunity is taken to place into synonymy an unused name proposed by Röding, the only name he introduced for a cancellariid.

In summary, a list is given of all known 18th Century species-level taxa in the Cancellariidae with synonyms.

DISCUSSIONS AND CONCLUSIONS

1. *Buccinum scalare* Gmelin, 1791 and *Murex scala* Gmelin, 1791.

Gmelin proposed the above names using identical figure references. His citations are as follows:

Murex scala (page 3551)
Mus. Lees. f. b.
Chem. Conch. 4. p. 1. vign. 37. f. a.b.c.

Buccinum scalare (page 3495)
Chemn. Conch. 4. p. 1. vign. 37. f. a.b.c.
Meussch. mus. Leens. f. b.
B) Knorr Vergn. 6. t. 17. f. 7.
Martini Conch. 4. 6. 122. f. 1130

Except for the order of the two primary references, and the references for the "variety" of *Buccinum scalare*, the two citations are the same. The short descriptions differ slightly, but seem to apply to the figures to which the names are applied herein. As the two figures cited represent two different identifiable species there appears to be no reason to ignore Gmelin's names. As discussed below, no long term usages will be disturbed by the adoption of these names which have long priority.

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The confusion surrounding these taxa was compounded by the inclusion of the Chemnitz vignette and a reference to *Buccinum scalare* Gmelin by Lamarck in his list of references for *Cancellaria scalarina* Lamarck, 1822. As shown herein, these references have been eliminated from the synonymy of Lamarck's species.

The reference cited by Gmelin as "Mus. Leess." and as "Meussch. mus. Leens." is a rare sales catalogue by F. C. Meuschen (1767) which lists the collection of Arnoud Leers.

Scalptia scala (Gmelin, 1791)

Murex scala Gmelin, 1791, p. 3551
Murex scala Gmelin, Bosc, 1801, 4:229 (reference to Chemnitz, Conch. 4, vign. 37, figs. a, b, c.)
Cancellaria costata Sowerby, 1833, p. 7, fig. 42 (*non C. costata* Sowerby, 1821).
Trigonaphera withrowi Petit, 1976, p. 39, pl. 2, fig. 3.
Scalptia withrowi (Petit), Abbott & Dance, 1982, p. 230, unnumbered figure.

Bosc (1801), by citing only the Chemnitz vignette, intentionally or unintentionally restricted Gmelin's taxon to those figures. Recognition of the three Chemnitz figures is possible only when it is realized that in these figures the shell is oriented with the apex tilted away from the viewer, and the area between the shoulder angle and the suture is not visible. Specimens of this West African species have become available in reasonable quantities only in the past few years or recognition of the Chemnitz figures certainly would have been made sooner. A specimen in the writer's collection matches these Chemnitz figures in details of sculpture and color, the only difference being that the illustrations are slightly elongated making the shell appear more attenuate. This is an artifact of the tilted position of the shell in the drawings and otherwise the delineation is excellent.

As the only other available name for this species has been in use for less than a decade there seems to be no reason why the Rules of Priority should not apply.

Trigonostoma scalare (Gmelin, 1791)

Buccinum scalare Gmelin, 1791, p. 3495
Trigona pellucida Perry, 1811, pl. 51
Delphinula trigonostoma Lamarck, 1822, 6(2):231
Cancellaria trigonostoma (Lamarck), Deshayes, 1830, 2:180; 1843, 9:409
Trigonostoma pellucida (Perry), Petit, 1967, p. 217.

Gmelin based this taxon on two figures, and a variety on two additional figures. Eliminating the references to what he considered to be a variety, and eliminating the Chemnitz reference which was Bosc's sole reference for *Murex scala* Gmelin, leaves only the Meuschen figure to represent *Buccinum scalare*. This rare Meuschen reference was apparently cited by no authors after Gmelin, and the single plate contains only two figures. Meuschen's figure b. is a very good drawing of the species later described as *Trigona pellucida* Perry and *Delphinula trigonostoma* Lamarck, and is here designated as representing the lectotype of *Buccinum scalare* Gmelin, 1791. This well-known but rare species is figured in the standard iconographies of Sowerby, Reeve, Kiener and Tryon. A color photograph is in Abbott & Dance (1982:229).

No locality was given by Gmelin or Lamarck, and Perry stated that it was from the "South Seas." Sowerby (1833:7) gave the location as Ceylon, which should be considered as the type locality. The species ranges from Ceylon to Queensland, Australia. Australian records are given by Garrard (1975:21) but he misidentifies the species as *T. antiquata* (Hinds, 1843).

Trigonostoma pellucida (Perry) has been used for this species only since 1967 and as it has appeared in very few works the Rules of Priority should be adhered to and the oldest name for the species, *T. scalare* (Gmelin), applied.

Deshayes (1843:403), in his convoluted attempt to conserve *Cancellaria scalarina* Lamarck which is discussed later in this paper, evidently recognized the possibility of *Buccinum scalare* being the same as *Cancellaria trigonostoma* (Lamarck) as he states: "*Pour le Buccinum scalare, dont il faudrait avant tout retrancher le variété, il faudra peut-être établir une troisième espèce qui a les plus grands rapports avec la Cancellaria trigonostoma.*"

2. *Buccinum pyrozonias* Gmelin, 1791 and *Cantharus triplicatus* Röding, 1798

Cancellaria (Bivetiella) cancellata (Linné, 1767)

Murex scabriculus Linné, 1758, p. 751
Voluta cancellata Linné, 1767, p. 1191 (*nom. subst. pro Murex scabriculus* Linné, 1758, *non Voluta scabriculus* (Linné, 1758)
Buccinum pyrozonias Gmelin, 1791, p. 3488 (ref. to "Martini, Conch. 3, t. 109, f. 1017").
Cantharus triplicatus Röding, 1798, p. 133 (ref. to "Martini, 3, t. 109, f. 1017").
Cancellaria (Bivetiella) cancellata (Linné, 1767), Petit, 1976, p. 34.

Buccinum pyrozonias Gmelin, based on Martini's plate CIX, fig. 1017, was used as a valid name by Dillwyn (1817:635) and Wood (1818:111; 1828:111). Pfeiffer (1840:28) and Hanley (1856:118) recognized the conspecificity of *Buccinum pyrozonias* and *Voluta cancellata*, and Gmelin's name has not appeared in later literature.

For *Cantharus triplicatus*, Röding not only referred to the same figure cited by Gmelin for *Buccinum pyrozonias*, but listed Gmelin's taxon as a synonym. *Cantharus triplicatus* Röding is thus a junior objective synonym of *Buccinum* *pyrozonias* Gmelin and a junior subjective synonym of *Cancellaria cancellata* (Linné).

Richardson, Abbott & Davis (1979:126) incorrectly list *Ampulla purpurea* Röding as referring to the aforementioned Martini figure. Röding's incomplete reference for *A. purpurea* is to Chemnitz, vol. 9, plate 118, figs. 1017 and 1018.

For a discussion of the two names used by Linné for this species, see Petit (1976:34).

A good argument could be presented to the effect that the Martini figure (volume 3, pl.109, fig. 1017) is actually intended to represent the species now known as *Cancellaria similis* Sowerby, 1833 and not the similar (hence the name) *C.cancellata* Linné. Such an argment would be fortified by the comments of Chemnitz and Dodge. Dodge (1955:100) in discussing *C. cancellata* states: "Martini did not describe or figure it, although it was a well-known shell to the conchologists of his day, and Chemnitz commented on this fact in figuring the species (1780–1795, vol. 11, p. 27, pl. 179, figs. 1727–1728) as follows: 'To my great astonishment I see that the well-known *Voluta cancellata* of Linnaeus, which we receive in fair numbers from the West Indies and the coast of Guinea, a clear figure of which is seen in Born's Testac. Mus. Caes. pl. 9. figs. 7, 8, has been up to now forgotten and passed over in this Conchylien work.'"

As the name *Cancellaria similis* Sowerby is firmly entrenched in the literature, and a petition to the I.C.Z.N. for its preservation would almost surely be successful, further inquiry along these lines is pointless, and it is in the best interests of nomenclatorial stability to leave *Buccinum pyrozonias* Gmelin mired in the synonymy of *Cancellaria cancellata* (Linné).

3. *Voluta nassa* Gmelin, 1791.

Scalptia nassa (Gmelin, 1791)

Voluta nassa Gmelin, 1791, p. 3464
Cancellaria nassa (Gmelin), Roissy, 1806, 6:13
Cancellaria lamellosa Hinds, 1843, p. 49; 1844, p. 43, pl. 12, figs. 15, 16
Not *Trigonostoma lamellosa* (Hinds), Garrard, 1975, p. 24, fig. 3(13).

Gmelin based his *Voluta nassa* on three references: Seba 3, pl. 53, fig. 42; Knorr 4, pl. 26, fig. 6; Martini 4, pl. 124, figs. 1172, 1173. Seba's plate 53 contains two figures with the number 42. The left-hand figure 42 is a species of *Nassarius*. The right-hand figure 42 is a dorsal view of the species later described as *Cancellaria lamellosa* Hinds. The two Martini figures are dorsal and ventral views of a *Nassarius*. The Knorr figure is a cancellariid, and with much imagination could be interpreted as a worn specimen of the species figured by Seba. It would appear that Gmelin had access to a specimen as the only ventral view among his references is that of a *Nassarius* yet in his description he states: "*Columella triplicata umbilicata*." However, Kohn (1966:75) has pointed out that the species names introduced by Gmelin were based entirely on published information, rather than on specimens. The description "*columella triplicata*" could have been taken from Martini (1780, 4:45), but the source of the descriptive "*umbilicata*" is problematical. As pointed out by Dodge (1959:172) and reiterated by Kohn (1966:76), the diagnosis should receive more weight than an indication in attempts to identify a nominal species. Gmelin's short description, together with the cited figure of Seba, is considered to be adequate for specific determination.

In introducing the name *Cancellaria scalarina*, Lamarck (1822, vol. 7:113) listed several references to figures and also included in the synonymy *Voluta nassa* Gmelin, with further reference to *Buccinum scalare* Gmelin. It was a fairly common practice in Lamarck's time to rename a species upon transfer from one genus to another, a practice that was fortunately short-lived. Deshayes, when revising Lamarck's work, went to great lengths to conserve Lamarck's names and in doing so added to already existing confusion. He recognized that the figures cited by Lamarck, which would include Gmelin's references for *V. nassa*, represented several species. His solution (Deshayes, 1843:403), which is taken as "first reviser" action, was to restrict *Voluta nassa* to the figures of Knorr and Seba and to restrict Lamarck's *Cancellaria scalarina* to the Martini figures. It should be noted here that Lamarck copied Gmelin's error in referring to Volume 4 of the Conchylien-Cabinet as being of Martini, as it was actually authored by Chemnitz. Sowerby (1833:7) had already cited, but not figured, *C. scalarina* Lamarck, giving as the sole reference these same Chemnitz figures. Deshayes (1843:410), in his discussion of *C. nassa*, which he attributes to Roissy, states that the species was recognized by Roissy and was figured by Knorr and Seba, but that he could not locate the species in the recent monographs of Kiener (1841) and Sowerby (1832–33). It would appear that he had a specimen in hand as he gave a rather detailed description that is at some variance with the figures cited. As it is impossible to make a specific identification from Deshayes' description, *Voluta nassa* Gmelin is here further restricted to the right-hand figure 42 of Seba which is here selected representative of the lectotype of *Voluta nassa* Gmelin and is considered to be conspecific with *Cancellari lamellosa* Hinds, 1843.

Although the name *Cancellaria lamellosa* was proposed over a century ago, its passing into synonymy should not cause any disruption of the literature. Literature citations for *C. lamellosa* since the standard iconographies of the 19th Century have been very few, and there is considerable confusion in these records. *Cancellaria lamellosa* Hinds was listed by Melvill & Standen (1901:451) from the Persian Gulf, but was not figured. Due to the confusion regarding the identity of species of *Scalptia*, and due to an almost total lack of detailed information as to the range and variability of species, it cannot be determined with certainty that the species they cited was in fact *C. lamellosa*. It has been reported from South Africa and Mozambique by Bartsch (1915:232), Barnard (1959:15) and Kensley (1973:194, fig. 754) but I consider these references to represent *Scalptia* *crossei* (Semper, 1861). For a discussion of this see Petit (1980:212). The most recent reference to *C. lamellosa* is that of Garrard (1975:24, fig. 3(13)), but the shell illustrated is not typical of the species and may represent another taxon.

Gmelin gave the locality of his *Voluta nassa* as "*S. Mauritii et Guineam*" which were localities cited by Chemnitz (1780:46). As the Chemnitz figures have been eliminated from the synonymy of *V. nassa* this locality citation has no meaning. Hinds (1843:49) did not cite a type locality for *Cancellaria lamellosa*, but stated that it had been found in the Indian Archipelago, the Cape of Good Hope, Ceylon, and in the Straits of Maccasar. He further stated that Cuming "procured specimens in seven fathoms, coarse sand, at the Island of Corregidor, in the Bay of Manila." Garrard's (1975:25) designation of the "Indian Archipelago" as type locality for *C. lamellosa* cannot be allowed to stand as the locality is too vague, and the only existing type material is from the Philippines. There are seven syntypes in the British Museum (Natural History), register numbers 1968414 and 1968415. The type locality for *C. lamellosa* is here designated as Island of Corregidor, Manila Bay, Philippines.

Cancellaria scalarina Lamarck, although restricted by Deshayes to the obviously nassariid figures of Chemnitz, is not a *Nassarius*. Deshayes' restriction is meaningless as Lamarck's holotype is in existence in the Museum d'Histoire Naturelle de Geneve, register number 1097/85 and it is a *Scalptia*. Although a photograph of the type is available, the specimen appears to be gerontic and specific identification with other taxa is not attempted at this time.

4. *Buccinum piscatorium* Gmelin, 1791 and *Murex semilunaris* Gmelin, 1791.

Cancellaria (Solatia) piscatoria (Gmelin, 1791)

Buccinum piscatorium Gmelin, 1791, p. 3496
Murex semilunaris Gmelin, 1791, p. 3549
Cancellaria nodulosa Lamarck, 1822, p. 113
Cancellaria piscatoria (Gmelin) Fischer-Piette, 1942, p. 218, plate 6, fig. 3.

Gmelin based *Buccinum piscatorium* on Chemnitz, volume 4, plate 124, figures 1151 and 1152, the same figures cited by Lamarck for *Cancellaria nodulosa. Murex semilunaris* was based on Adanson's plate 8, figure 15. The Chemnitz figures are recognizable, but are not as good as the Adanson figure. Although the synonymy of *B. piscatorium* and *C. nodulosa* was recognized very early (Sowerby, 1833:5), Kiener (1841:15) and Deshayes (1843:404) attempted to conserve Lamarck's name. However, they were the only authors to give *C. nodulosa* priority.

Although Adanson's work was well known and his illustrations of good quality, Gmelin's *Murex semilunaris* does not appear to have been mentioned by any author prior to Fischer-Piette (1942:218) who properly placed it in the synonymy of *Cancellaria piscatoria* (Gmelin) which has page priority.

This West African species is the type of the genus-level taxon *Solatia* Jousseaume, 1887.

5. 18th Century species-level taxa in Cancellariidae.

This annotated list is believed to be complete for all binomina proposed prior to 1801.

Murex scabriculus Linné, 1758 = *Cancellaria cancellata* (Linné, 1767)

Buccinum evulsum Solander, 1766 = *Admetula evulsa* (Solander, 1766). Eocene, Europe. Type of *Admetula* Cossmann, 1889.

Voluta cancellata Linné, 1767 = *Cancellaria (Bivetiella) cancellata* (Linné, 1767). Recent, West Africa. Type of *Bivetiella* Wenz, 1943.

Voluta reticulata Linné, 1767 = *Cancellaria reticulata* (Linné, 1767). Recent, Caribbean. Type of *Cancellaria* Lamarck, 1799.

Tritonium viridulum Fabricius, 1780 = *Admete viridula* (Fabricius, 1780). Recent, Circumboreal.

Voluta nassa Gmelin, 1791 = *Scalptia nassa* (Gmelin, 1791). Senior subjective synonym of *Cancellaria lamellosa* Hinds, 1843. Recent, Indo-Pacific.

Buccinum pyrozonias Gmelin, 1791 = *Cancellaria cancellata* (Linné, 1767).

Buccinum scalare Gmelin, 1791 = *Trigonostoma scalare* (Gmelin, 1791). Senior subjective synonym of *Trigona pellucida* Perry, 1811, and of *Delphinula trigonostoma* Lamarck, 1822, the type of *Trigonostoma* Blainville, 1827. Recent, Indo-Pacific.

Buccinum piscatorium Gmelin, 1791 = *Cancellaria (Solatia) piscatoria* (Gmelin, 1791). Recent, West Africa. Type of *Solatia* Jousseaume, 1887.

Murex semilunaris Gmelin, 1791 = *Cancellaria (Solatia) piscatoria* (Gmelin, 1791).

Murex scala Gmelin, 1791 = *Scalptia scala* (Gmelin, 1791). Senior subjective synonym of *Trigonaphera withrowi* Petit, 1976. Recent, West Africa.

Cantharus triplicataus Röding, 1798 = *Cancellaria cancellata* (Linné, 1767).

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REGENERATION OF THE PROBOSCIS, RADULA AND ODONTOPHORAL CARTILAGE OF THE SOUTHERN OYSTER DRILL *THAIS HAEMASTOMA CANALICULATA* (GRAY) (PROSOBRANCHIA: MURICIDAE) AFTER AMPUTATION

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ABSTRACT

The ability of *Thais haemastoma canaliculata* (Gray) to regenerate a fully functional proboscis, radula, odontophore, and radular sac after complete amputation of all structures was investigated. All drills from which the radular mechanism was removed, completely recovered from the anesthesia and surgery and were actively moving about the tank within one day post amputation. Snails resumed feeding only after the entire radular mechanism was completely regenerated. The entire regenerative process occurred within four to five weeks post-amputation. These drills exhibited normal feeding behavior and produced normal boreholes in oyster shells. The regenerated radula and its accessory structures were normal in appearance and closely resembled original structures except for size; the regenerated structures were slightly smaller in size than their original complements.

Muricid gastropods possess the ability to regenerate lost organs. Regeneration of the proboscis and radula has been studied in several species of muricids (Demoran and Gunter, 1956; Carriker et al., 1972). Carriker et al. (1972) conducted a comprehensive investigation of the ability of *Urosalpinx cinerea* (Say) and *Eupleura caudata etterea* Baker to regenerate their proboscis after amputation. These snails were capable of regenerating both the radula and proboscis. Demoran and Gunter (1956) reported the same regenerative ability in the southern oyster drill *Thais haemastoma* (Lamarck); however, in their short note they mentioned no qualitative or quantitative observations of the regenerated proboscis and radula as compared to the original structures. There is a paucity of information concerning regenerative ability in *Thais* sp. after extensive damage to the proboscis (i.e., complete amputation of radula, odontophore, and radular sac).

The objectives of this investigation were to (1) observe the structure of the radula of *T. haemastoma canaliculata* (Gray) (Abbott, 1974) using scanning electron microscopy; (2) determine if the proboscis, radula, and odontophoral cartilage will regenerate after complete amputation of these structures; (3) observe morphological differences between original and regenerated structures; (4) determine the time interval necessary for complete regeneration of these structures; and (5) determine the time when post-amputation feeding by the snails resumes.

MATERIALS AND METHODS

Seventy adult oyster drills (mean shell length = 61.6 mm) were collected at Grand Isle, Louisiana, U.S.A. The snails were transported to the laboratory and placed into two 38 L aquaria at room temperature (23–25°C and 20‰ salinity (Instant Ocean® Sea Water Mix). Fifty snails (male:female = 1:1) were placed in one aquarium (tank A) to be used in the determination of the time and extent of regeneration of the proboscis. Plexiglas dividers were used in the second aquarium (tank B) to separate the remaining 20 snails (one snail/chamber) that were used to determine the post-probosectomy time at which feeding would resume. The male-to-female ratio in tank B was also 1:1. Both tanks were aerated throughout the experiment. The snails were allowed two weeks to acclimate to the laboratory conditions before the experiment began. Oysters (*Crassostrea virginica* [Gmelin]) and clams (*Rangia cuneata* [Sowerby]) were provided as prey during the acclimation period. Empty oyster shells from tank B were saved for a scanning electron microscopy (SEM) investigation of bore holes.

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Magnesium sulfate was not an effective narcotizing agent for *T. haemastoma canaliculata* in that it took a high concentration of the substance to anesthetize the snails and also required an extensive period of time to take effect. More importantly, the snails did not protrude their proboscides under $MgSO_4$ treatment, which was required for a complete amputation. Sevin® dust (1-napthyl-N-methylcarbamate) was finally chosen as an appropriate anesthetic agent (Carriker and Blake, 1959). Snails were placed in 3 L of a 1 ppm solution of Sevin® in 20°/ooS sea water. Sevin® was first dissolved in a minimal amount (15 ml) of acetone before mixing with sea water. Approximately one hour was required for complete anesthetization. Drills were considered completely anesthetized (Fig. 1) when they fully extended their proboscis for more than half of their body length. The proboscis of each snail was pulled gently with a pair of fine forceps to further extend it and was then amputated at its base with a pair of iris scissors. Each proboscis was prepared for either SEM or light microscopy. All proboscides were examined after amputation to insure complete removal of all radular structures. After probosectomy, each drill was returned to its tank where full recovery from anesthesia occurred within two days. The snails were considered recovered when actively moving about. There were no observable effects from the anesthesia.

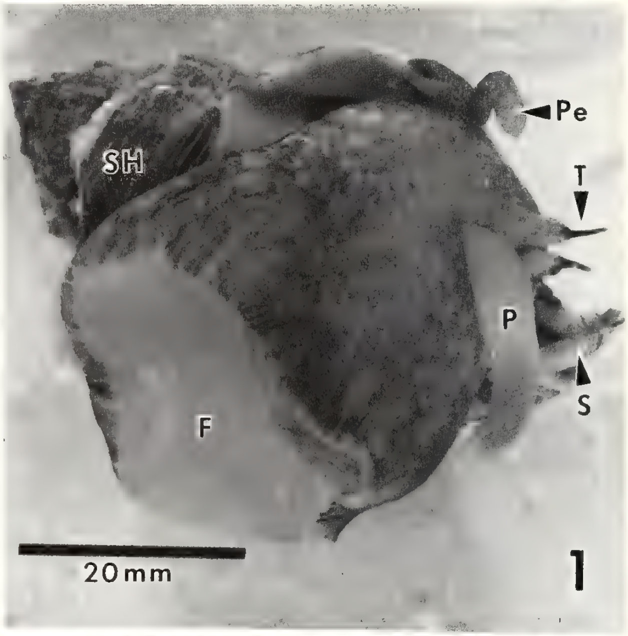
After drills completely recovered from anesthesia, live oysters were placed in both tanks. Oysters were examined daily for any evidence of predation and were regularly replaced with fresh oysters.

Five snails were sacrificed from tank A per week for ten weeks and examined for evidence of regeneration. All regenerated material was preserved for later histological examination. The sex of each snail was also determined at that time.

When an oyster from tank B showed evidence of snail predation (bore holes; Fig. 2), it was removed from the tank and the number of the snail feeding upon it was recorded. Snails from tank B that had preyed upon oysters were sacrificed and their regenerated proboscides were prepared for microscopical examination.

For SEM the original and regenerated proboscides of drills were dissected by making a longitudinal cut through the dorsal epithelium and muscle layers to expose the radulae and odontophores. The tissues were fixed overnight with 2.5% gluteraldehyde in 0.2M sodium cacodylate-sucrose buffer (585 mOsm; pH = 8.0). Specimens were rinsed for 1 h in three changes of distilled water to remove all buffer salts, dehydrated in acidified 2,2-dimethoxypropane, critical-point dried in CO_2, and sputter-coated with 200Å of gold-palladium. Specimens were then examined with a Hitachi S-500 SEM at 25 KV.

Oyster shells from tank B were prepared for SEM study by air drying followed by critical-point drying in CO_2. Shells were then sputter-coated with 200Å of gold-paladium.



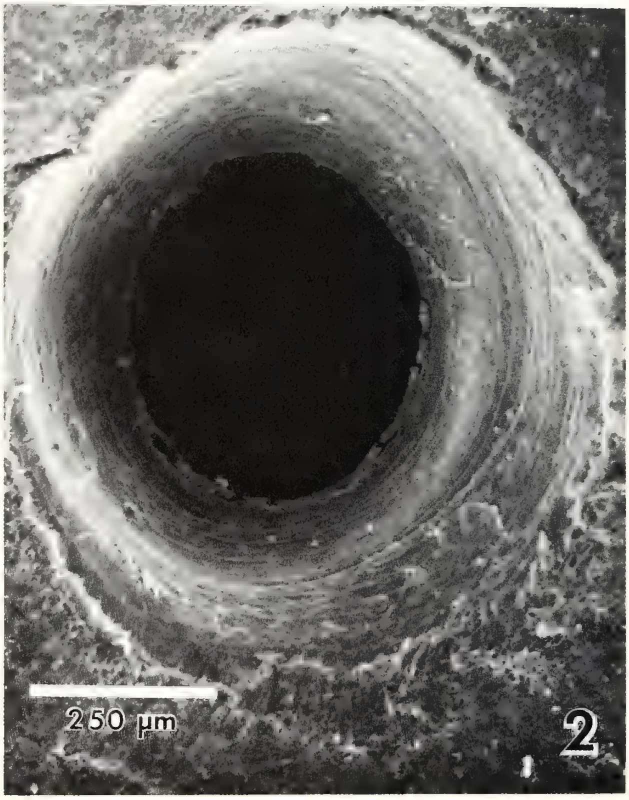


Fig. 1. Anesthetized oyster drill, *(Thais haemastoma canaliculata)* after 1 h in 1 ppm Sevin®: F = foot; P = extended proboscis; Pe = penis; S = siphon; SH = Shell; T = tentacles. **Fig. 2.** Borehole in shell of oyster *Crassostrea virginica* made by snail in Fig. 1.

For light microscopy the proboscis of each drill was fixed in formalin-acetic acid-alcohol (FAA) overnight, dehydrated in ethanol, cleared in xylene, and embedded in paraffin. Sections (10 μm) were stained with azan (Humason, 1972).

The following measurements (Fig. 3) were made on original and regenerated radulae of ten snails: mean radular width, mean radular length, mean total width of rachidial teeth, mean length/width of central rachidial cusp, mean width of individual lateral cusp, and mean odontophore width. Differences between original and regenerated radulae were compared by a paired t-test.

RESULTS

The radular and odontophoral cartilage of *Thais haemastoma canaliculata* lies within a long, muscular sheath known as the proboscis (Fig. 1). The proboscis and radula of *T. haemastoma* are very similar to those of *Urosalpinx cinerea* described by Carriker (1943). The proboscis (Figs. 4,5,6) is composed of an outer thick layer of circular muscle surrounding two inner layers of oblique muscle. Lining the lumen of the proboscis is a thick layer of longitudinal muscle. The proboscis sheath is covered by a mucous-secreting epithelium containing many goblet-type cells. The proboscis contains myoglobin giving the distal end a reddish appearance. The radular and odontophoral cartilage (Figs. 8,10,11) lies within the distal one-third of the proboscis with many associated nerves and muscles for the protrusion and retraction. The radula of *T. haemastoma* like that of *U. cinerea* (Carriker, 1943; Carriker et al., 1972) is of the rachiglossan type (Fretter and Graham, 1962) and is composed of three rows of longitudinal teeth: a central row of five-cusped, rachidial teeth and two lateral rows of single-cusped, marginal teeth (Fig. 9). The radula lies on the radular membrane that covers the odontophoral cartilage (Figs. 8,11). The proximal portion of the radula is enclosed within a radular sac that curves 180° distally and is attached by muscles to the proximal base of the odontophore (Figs. 8,10). The radular teeth of *T. haemastoma*, like those of most oyster drills (Carriker, 1943 et al. 1972; Fretter and Graham, 1962) point "backwards" or proximally (Figs. 8,9,11). The radula is protruded out of the proboscis, placed against the substratum or food to be scraped, and then retracated back over the odontophore, thus pulling food and other particles (Carriker, 1977) into the buccal area for swallowing (Fig. 8). As old teeth are worn down at the distal portion of the radula new teeth are secreted proximally within the radular sac.

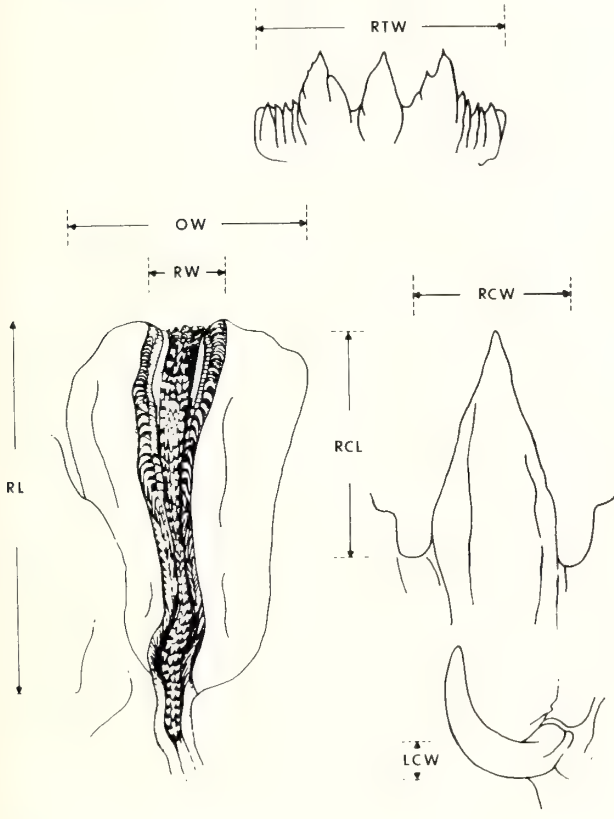


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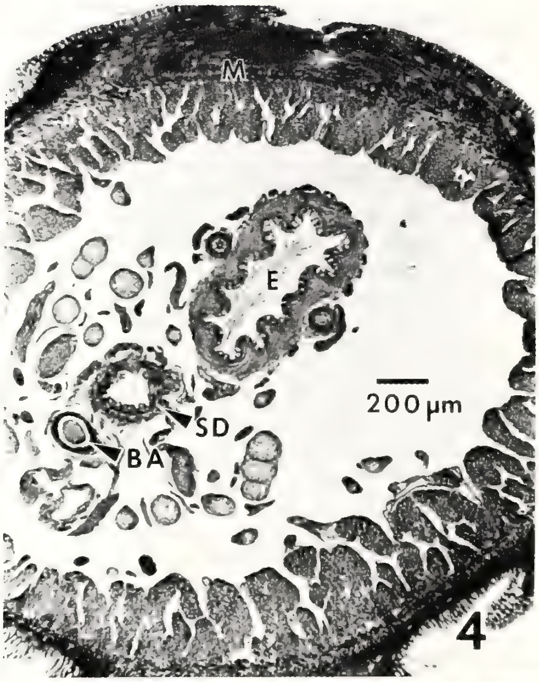
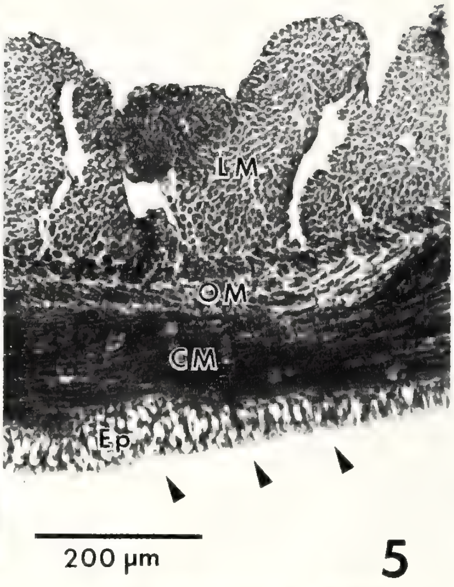
Fig. 3. Measurements of radula and odontophore of *Thais haemostoma canaliculata*: RTW = rachidial tooth width; OW = odontophoral width; RW = radula width; RCW = central rachidial cusp width; RL = radula length (over odontophore); RCL = central rachidial cusp length; LCW = lateral cusp width.

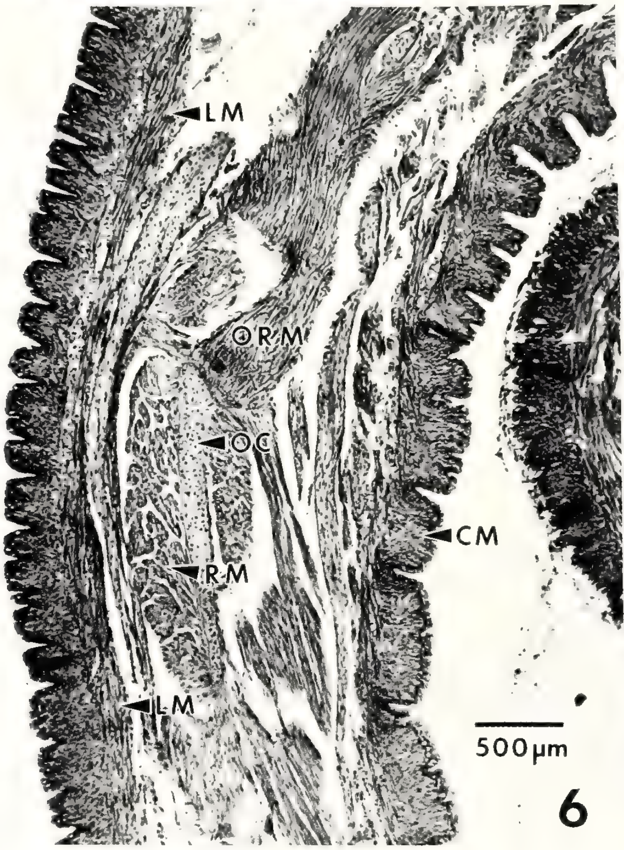
The odontophore (Figs. 6,7,8,11) is the supportive base for the radula (Fretter and Graham, 1962) and is reinforced by cartilage. The odontophore and perhaps the radular sheath appear to have associated myoglobin, giving both a dark reddish color.

All snails completely recovered from the anesthesia and were actively moving about the tank within 24 hours post-narcotization. All snails survived until they were sacrificed for examination at the end of the experiment. During narcotization, volume regulation of the drills was apparently hampered; the foot swelled extensively (Fig. 1). The snails recovered from this side effect. It is probable that the drills metabolized small amounts of the Sevin® without any permanent ill effects. The complete radular structure (radula, odontophore, and radular sac) was completely removed from all snails because none of the components were found in the stump of the proboscis.

Within two to five days post-amputation a mass of undifferentiated cells similar to that which Carriker et al. (1972) observed, formed over the stump of the old proboscis. Approximately two weeks post-amputation evidence of proboscis regeneration was observed; a small portion of a new proboscis was formed at the distal end of the old stump. The new proboscis was pale and white due to the absence of myoglobin. This new proboscis increased in length over the following two weeks. Myoglobin first appeared in the proboscis approximately three to four weeks post-amputation. The radula and odontophore of all snails completletly regenerated within four to five weeks post-amputation. Evidence of odontophoral regeneration was observed before radular regeneration occurred (Fig. 7).







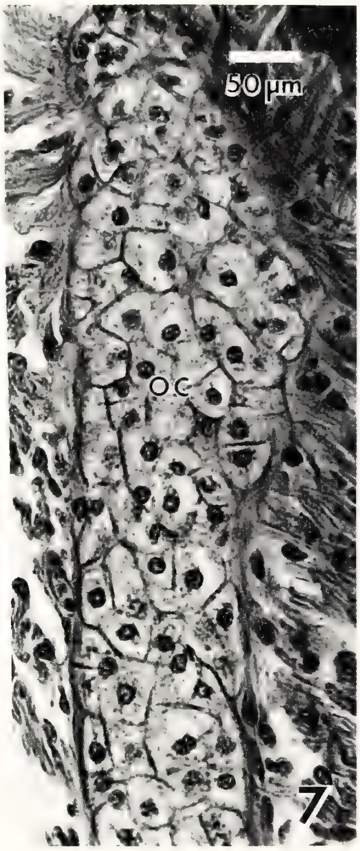
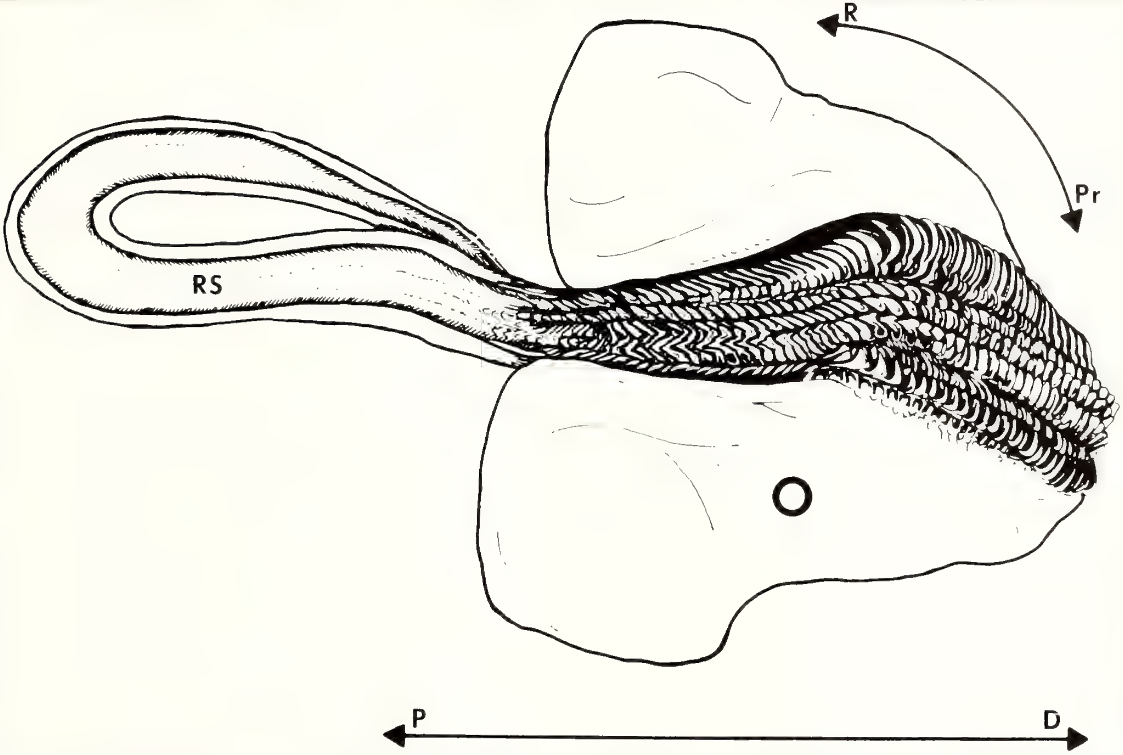


Fig. 4. Cross section of proboscis of *Thais haemastoma canaliculata* proximal to radula: M = muscle layers in proboscis wall; E = esophagus; SD = salivary duct; BA = buccal artery. **Fig. 5.** Cross section of wall of proboscis: LM = longitudinal muscle layer; OM = oblique muscle layer; CM = circular muscle layer; Ep = epithelium. Arrows indicate mucous on epithelium. **Fig. 6.** Longitudinal section of proboscis prior to complete radular regeneration: LM = longitudinal muscle layer; ORM = odontophore retractor muscle; OC = regenerated odontophoral cartilage; CM = circular muscle layer; RM = radular membrane. **Fig. 7.** High magnification of the regenerated odontophoral cartilage (OC) in figure 6.



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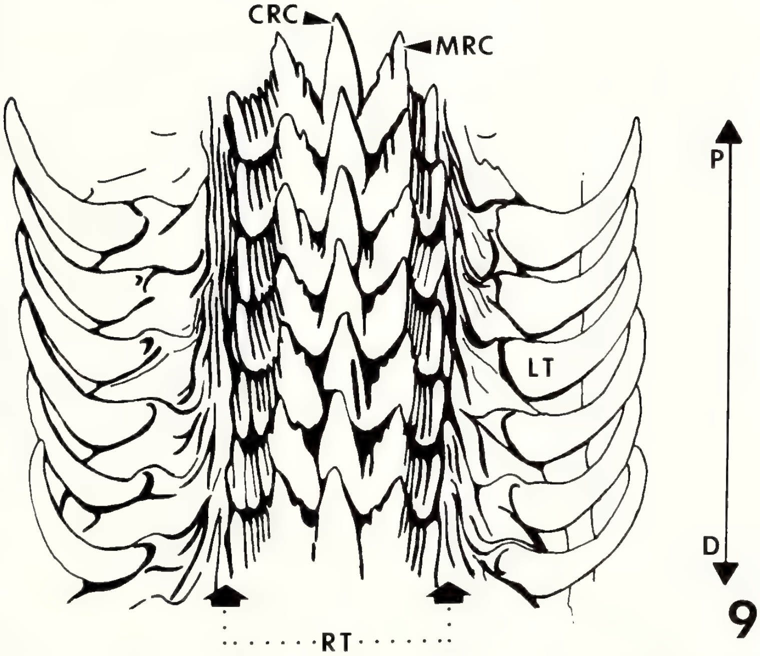

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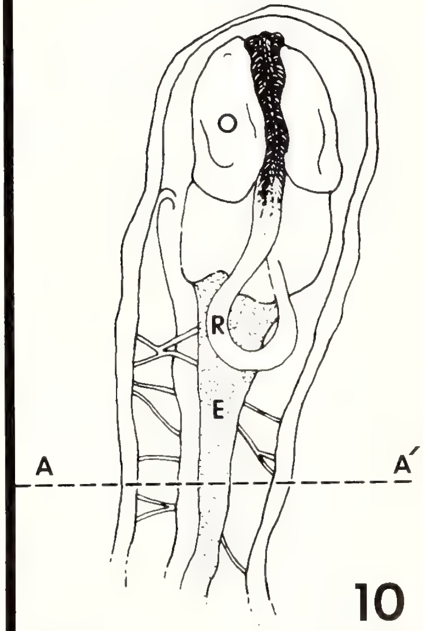

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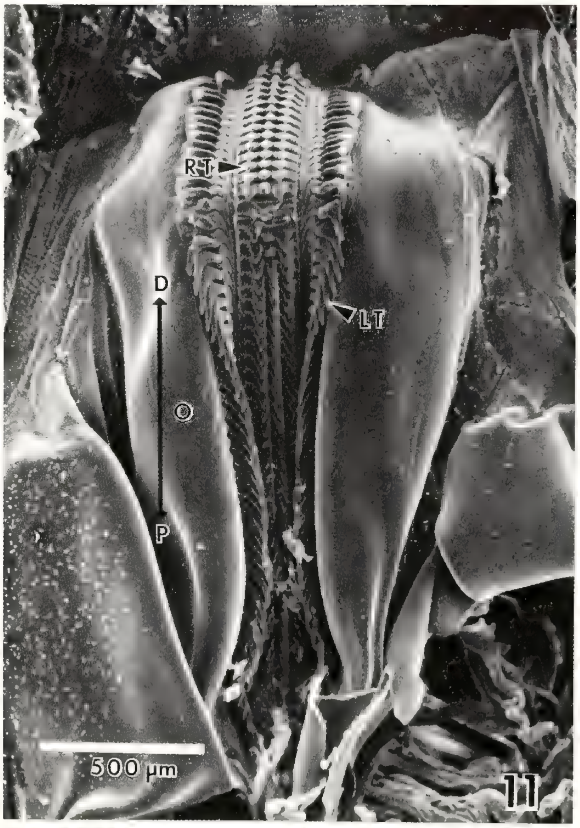
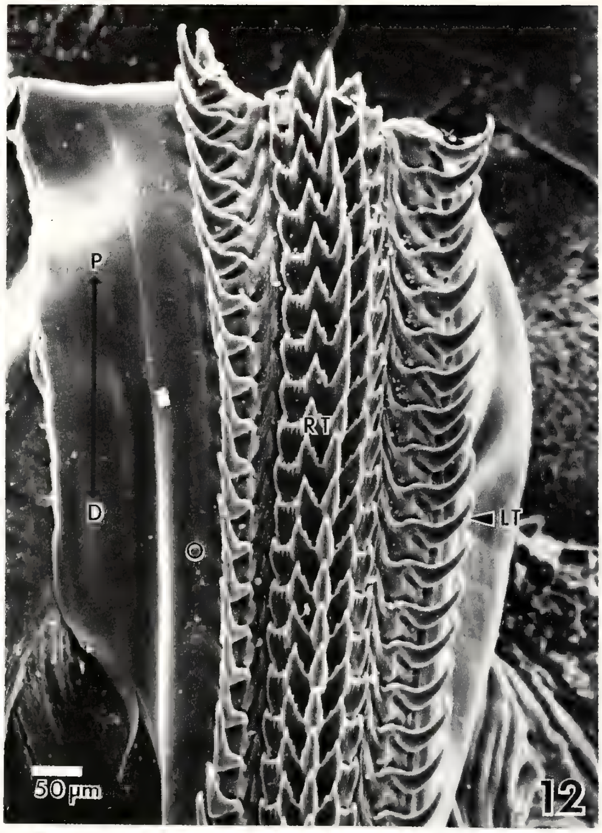
Fig. 8. Diagram illustrating typical radula, odontophore (O), and radular sac (RS) of *Thais haemastoma canaliculata:* R = direction of retraction of radula during drilling; Pr = direction of protrusion of radula during drilling; P = proximal; D = distal; Horizontal field width = 3.5 mm. **Fig. 9.** Drawing of a section of the radula of *Thais haemastoma canaliculata* illustrating the classification and orientation of the teeth: CRC = central rachidial cusp; MRC = marginal rachidial cusp; LT = lateral teeth; RT = rachidial teeth margin; P = proximal; D = distal. Horizontal field width = 550 μm. **Fig. 10.** Diagram of proboscis and contents during amputation: A–A′ = plane of amputation; O = odontophore; R = radular sac; E = esophagus (cut). Horizontal field width = 6.1 mm.


RT
D
LT
O
P
500 µm
11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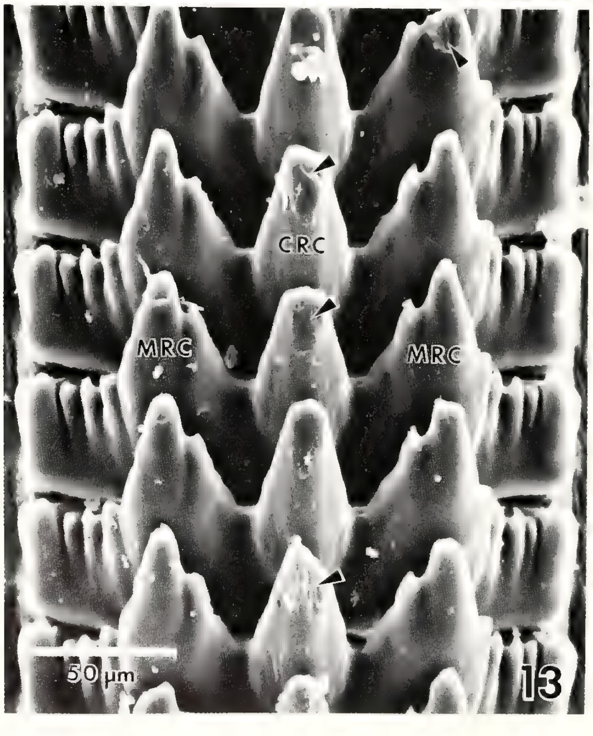
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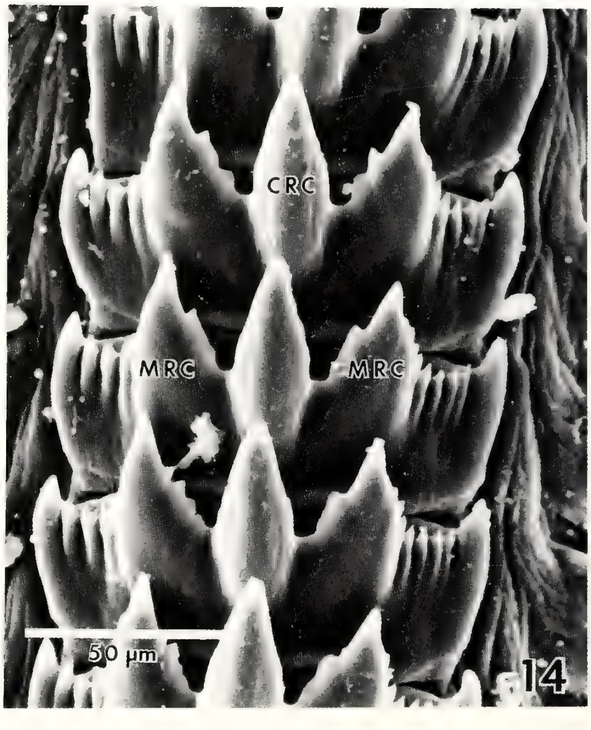
CRC
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MRC
50 µm
14

Fig. 11. Original radula and odontophore (O) of oyster drill: RT = rachidial teeth; LT = lateral teeth; D = distal; P = proximal. **Fig. 12.** Regenerated radula and odontophore (4.5 weeks post-amputation) of the same oyster drill in Fig. 11: RT = rachidial teeth; LT = lateral teeth; O = odontophore; P = proximal; D = distal. **Fig. 13.** Rachidial teeth of original radula (Fig. 11): CRC = central rachidial cusps; MRC = marginal rachidial cusps. Arrows indicate wear-marks on cusps. **Fig. 14.** Rachidial teeth of regenerated radula (Fig. 12). Note absence of wear marks on teeth: CRC = central rachidial cusps; MRC = marginal rachidial cusps.

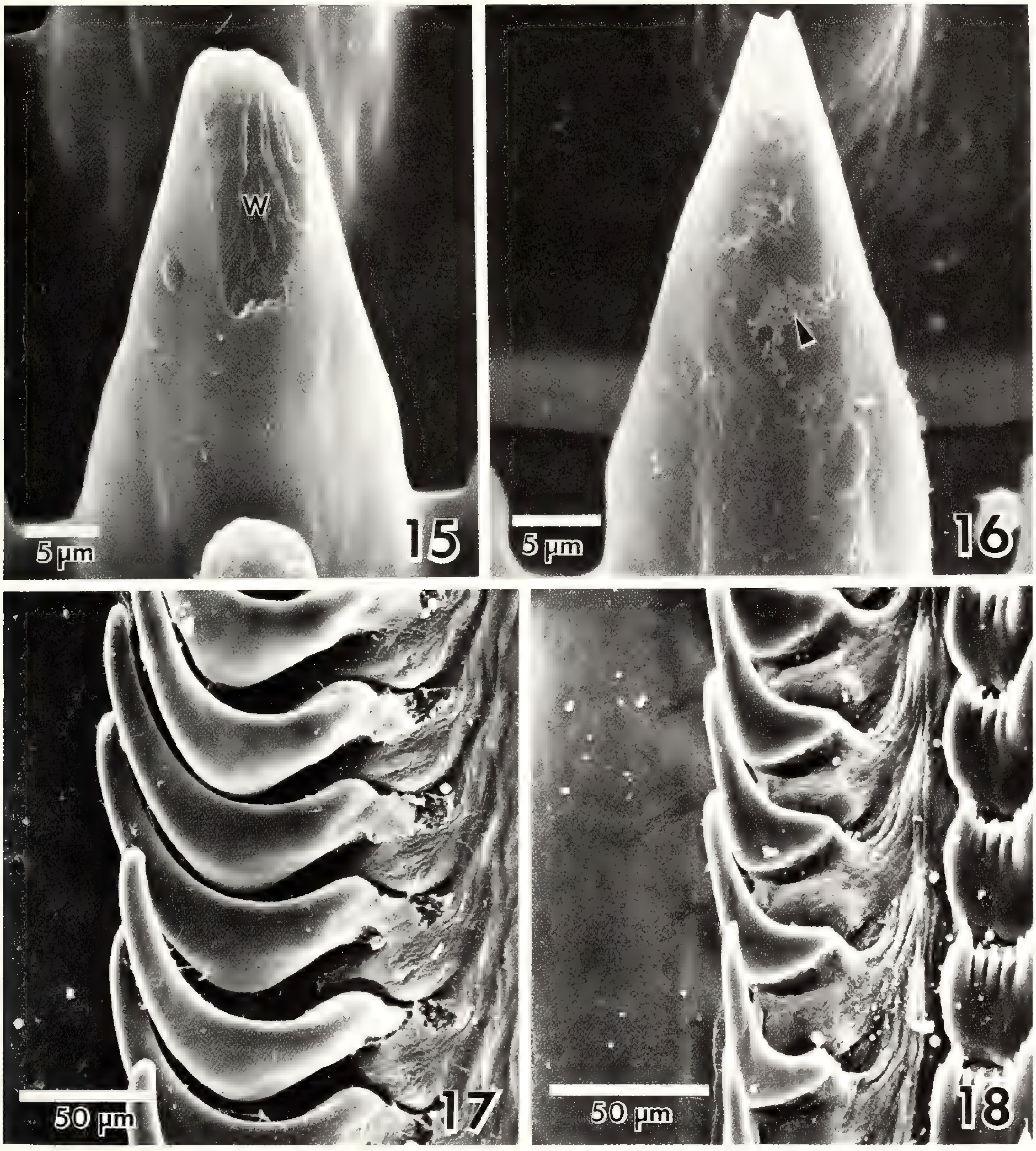

Fig. 15. Original central rachidial cusp of teeth in Fig. 13: W = wear on cusp. **Fig. 16.** Regenerated central rachidial cusp of that in Fig. 14. Arrow indicates mucus on cusp. **Fig. 17.** Lateral teeth of original radula (Fig. 11). **Fig. 18.** Lateral teeth of regenerated radula (Fig. 12).

The regenerated radulae were smaller in size than the original radulae. The size difference is illustrated by SEM micrographs (Figs. 11–18). All regenerated radulae and supportive structures were normal in all respects (Figs. 11–18). No apparent major morphological difference existed between the original and regenerated radulae of any snail with the exception of the amount of wear on the teeth. The original radula of each drill showed more obvious wear on the cusps than the regenerated radula (Figs. 13,14). This wear was especially pronounced on the central rachidial cusps (Figs. 13,15). Size differences between the original and regenerated radulae of the 10 measured snails were observed (Fig. 3). Significant differences ($\alpha = 0.05$) existed between the original and regenerated radulae in radula length, radular width, individual lateral teeth width, central rachidial cusp length, central rachidial cusp width, total rachidial teeth width, and odontophore width (Table 1). No significant difference ($\alpha = 0.05$) existed in the length/width ratio of the central rachidial cusp between original and regenerated teeth.

All 20 snails in tank B resumed feeding within approx-

Table 1. Measurements (μm) of original (O) and regenerated (R) radulae of *Thais haemastoma*. Measurements of regenerated radulae were taken at four weeks post-amputation.

Measurement	O—Radulae	R—Radulae	T Value
Radular Width	406.0 ± 24.50*	274.0 ± 53.70	4.24†
Radular Length	1577.0 ± 70.90	1125.0 ± 57.90	6.67†
Rachidial Teeth Width	153.0 ± 6.33	113.0 ± 5.85	5.51†
Central Rachidial Cusp Length	46.0 ± 6.46	28.1 ± 4.40	5.26†
Central Rachidial Cusp Width	26.0 ± 2.40	16.2 ± 1.96	6.40†
Central Rachidial Cusp Length/Width	1.7 ± 0.15	1.7 ± 0.13	−0.19
Lateral Cusp Width	27.0 ± 2.60	16.3 ± 1.30	3.44†
Odontophore Width	1635.0 ± 88.90	1035.0 ± 87.00	8.08†

*Mean ± S.E.
†Statistically significant at $\alpha = 0.05$.

imately four weeks (28.8 + 0.28 days) post-amputation. All drills in tank B regenerated a complete, normal-appearing radula, odontophore, and proboscis at the time feeding resumed. No observable differences existed in regeneration time or in the morphological features of the regenerated structures between male and female drills. Likewise, no significant difference (paired t-test; $\alpha = 0.05$) existed in the time to resumption of boring between the two sexes.

An interesting anomaly was seen in the radula of one of the drills examined. The central row of rachidial cusps was much reduced throughout the entire radular length compared to that of the 59 other snails examined (Fig. 19). Originally, we believed that this aberration resulted from wear during drilling and feeding; however, the regenerated radula of the same drill exhibited the same structural malformation (Fig. 20).

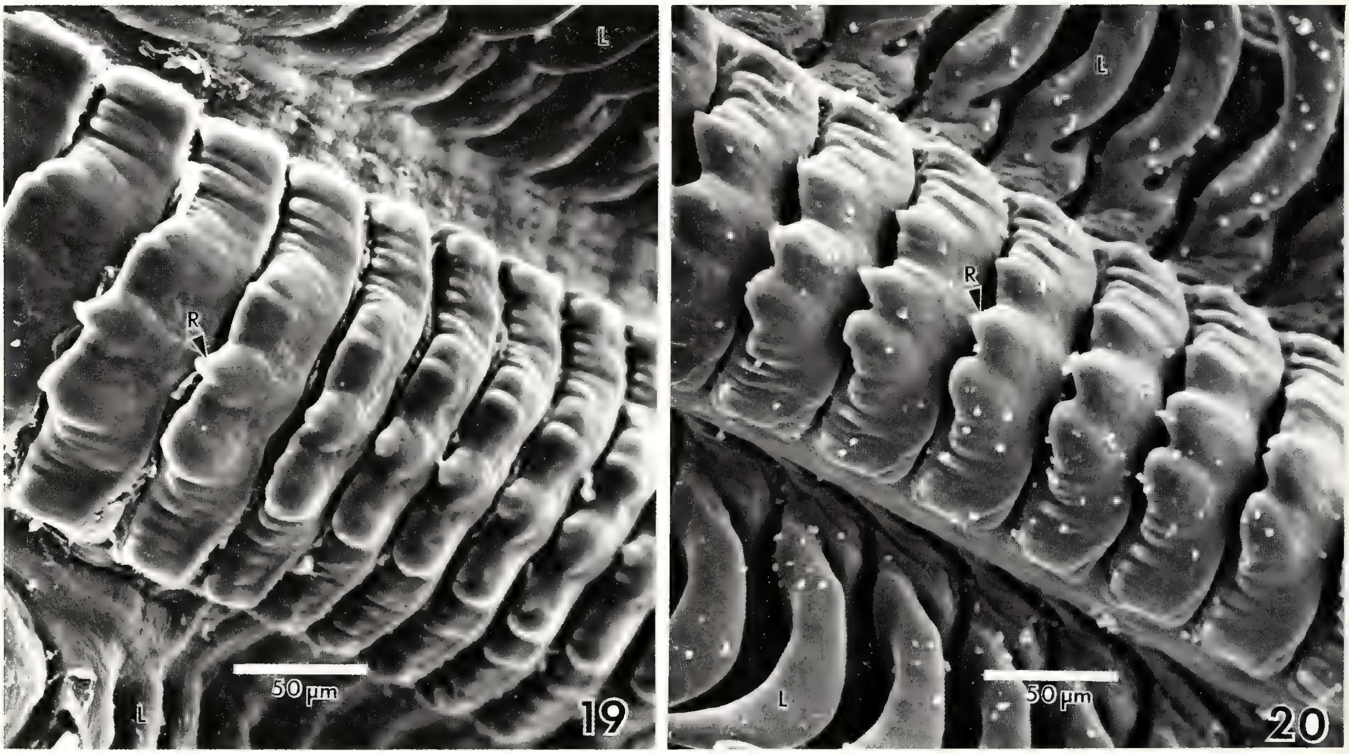

Fig. 19. Original radular anomaly found in one oyster drill: L = lateral teeth; R = reduced central rachidial cusp row. **Fig. 20.** Regenerated radular anomaly of same snail in Fig. 19: L = lateral teeth; R = reduced central cusp row.

DISCUSSION

The southern oyster drill is a euryhaline, estuarine gastropod found along the coasts of the Gulf of Mexico and southeastern United States. It preys primarily on barnacles and oysters (*C. virginica* and *Ostrea equestris* [Say]) but will also consume the rangia clam (*Rangia cuneata*) in the laboratory. The drill utilizes three organs in the feeding process: the radula, the accessory boring organ, and the hypobranchial gland. The drills use the radula and the accessory boring organ to excavate a hole near the outer margin of the shell of adult oysters. The radula provides the mechanical scraping action to create the borehole; however, the radula is not sufficiently strong to create the hole by itself. Carriker and his associates (Carriker, 1978; Carriker et al., 1978a; and Carriker et al., 1978b) demonstrated that the accessory boring organ in *U. cinerea* produces a chemical secretion that dissolves areas of the outer shell matrix which is then scraped away by the radula. Webb and Saleuddin (1977) observed the borehole formation process in *Nucella* (syn. *Thais*) *lapillus* (Linné) including enzymatic secretions from the accessory boring organ. This appears to be the same drilling pattern that occurs in *T. haemastoma canaliculata*; thus, shell drilling is accomplished by an alternating series of mechanical scraping and chemical dissolution activities. The reader is referred to Carriker (1981) for a complete description concerning the mechanisms of shell penetration and feeding by muricacean and naticacean predatory gastropods.

As mentioned previously *T. haemastoma canaliculata* will usually drill a hole near the ventral margin of the adult oyster shell. Smith (1983) also reported the same bore hole location on adult oysters consumed by *T. haemastoma canaliculata*. We observed that *T. haemastoma canaliculata* will occasionally drill through the central area of the shell and not at the ventral margin when feeding upon oyster spat which have noticeably thinner shells than adult oysters. Snails also drilled through the thick portions of the shell of other individual snails during starvation-induced cannibalism. During cannibalism it is the small snail that is usually eaten. Apparently, *T. haemastoma canaliculata* cannot efficiently drill through the thick central region of adult oysters; therefore, the boreholes are restricted to the thinner outer margin of the adult oyster shell. *Nucella* (syn. *Thais*) *lamellosa* (Gmelin), in contrast, can drill its normal prey, the relatively thin-shelled, blue mussel *Mytilus edulis* Linné (Carefoot, 1977).

During drilling the radula slides over the odontophore and is extended out of the mouth and then retracted back across the substrate (Fig. 8). The drilling process is actually a double action consisting of the odontophore "licking" across the substrate and the radula being drawn back over the odontophore (Carriker, personal communication); thus, the actual effective drilling is accomplished during the retraction stroke. The snail may swallow portions of the shell that are scraped off during retraction. Carriker (1977) provided evidence that *U. cinerea* swallows shell particles rasped off during drilling.

Carriker et al. (1974) analyzed the radular function of *U. cinerea follyensis* Baker by slow-motion photography and scanning electron microscopy. After *T. haemastoma canaliculata* drills a hole in the oyster shell, a paralytic toxin of urocanylcholine (Whittaker, 1960) is released from the hypobranchial gland of the snail into the mantle cavity of the oyster. This toxin paralyzes the oyster's adductor muscle causing the oyster valves to gape. Shell gape allows the snail access between the valves to the soft tissues of the prey. McGraw and Gunter (1972) suggested that perhaps *T. haemastoma* does not need the borehole to feed upon the oyster; instead, the paralytic secretion enters through natural gaps in the margin of the oyster shell causing the oyster to gape. This may have happened in a few instances; however, from the results obtained with the probosectomized snails in tank B, we believe that the proboscis does play an important role in the actual drilling of the shell. The most important point is that the drills need the radular apparatus to ingest the oyster flesh regardless of the method of shell entry. None of the 20 probosectomized snails fed until a complete, functional proboscis and radular mechanism were regenerated, and all oysters that were consumed exhibited boreholes. We often observed several snails feeding on a single large oyster. Smith (1983) found that small oyster drills (1.5–2.5 cm long) produced more boreholes in juvenile oysters than large drills (6.0–7.0 cm long) produced. Smith suggested that small oyster drills may not secrete enough paralytic toxin to cause the oyster valves to gape. It is possible that during predation large oysters require a greater amount of paralytic toxin than one snail is capable of producing. It is probably more advantageous therefore, for several snails to simultaneously attack a large oyster. This may also explain why we usually observed one borehole on small oyster spat and multiple holes on large adult oysters.

Isarankura and Runham (1968) reported on the normal replacement of gastropod radular teeth that are worn during feeding. Our results on *T. haemastoma canaliculata* indicate that radular teeth are progressively worn during the drilling process and must be continuously replaced. The regenerated radula of *T. haemastoma canaliculata* showed no signs of wear (Figs. 12,14,16,18); whereas, the old radula of the same snail showed extensive wear, especially on the central rachidial cusps (Figs. 11,13,15,17). We believe that in *T. haemastoma canaliculata* as in other gastropods (Fretter and Graham, 1962) new teeth are secreted proximally to replace the older, distal radular teeth that are worn down during drilling and feeding.

Carriker et al. (1972) found that regeneration of the proboscis and radular mechanism of *U. cinerea* and *Eupleura caudata* Say was rapid and uniform; resumption of boring varied from 11 to 34 days post-amputation. Their experimental temperature varied between 23.5 and 33.0°C; that variation may explain the wide range of regeneration times. Demoran and Gunter (1956) indicated that *T. haemastoma* could regenerate its proboscis in three weeks after having only the distal portion of the proboscis amputated. Our results agree closely with those of Carriker et al. (1972). We demonstrated that *T. haemastoma canaliculata* can regenerate a complete, fully functional radular mechanism (radula, odontophore, and radular sac) at 23 to 25°C within four to five weeks after complete amputation.

Several factors may account for the differences reported for the regeneration time of the radular mechanism in *T. haemastoma* by Demoran and Gunter (1956) and us. Since Demoran and Gunter (1956) reported that they were able to amputate only the distal portion of the radula, it is quite probable that in their experiment a portion of the regenerative tissue of the radular sac was left behind in the stump of the old proboscis. This is plausible since the radular sac is very long and extends proximally for some distance before curving back toward the odontophore (Figs. 8,10). It is possible that this situation also occurred in the amputation and regeneration experiments of Carriker et al. (1972). In our investigation the method of drill anesthetization permitted complete amputation of the radula, odontophore, and all of the radular sac (Fig. 10). The probosectomized snails in our experiment were able to regenerate a complete radular apparatus from the remaining stump of the original proboscis. The possible presence of a residual piece of the radular sac in the stump of the original proboscis might help to explain the discrepancy between the regeneration time reported for *T. haemastoma* by Demoran and Gunter (1956) and in this study. If a piece of radular sac tissue remained in Demoran and Gunter's snails, then those snails could have regenerated a complete radular mechanism in less time than a drill from which all of the original radular mechanism had been completely removed; hence their three week regeneration time and our four to five week regeneration time are not out-of-line. The use of Sevin® as the anesthetic agent may have slowed the regenerative process of the snails in our investigation; however, the snails recovered so quickly we do not believe that Sevin® alone can explain the difference in regenerative time. Since Demoran and Gunter did not report experimental temperatures, we assumed that it was done at room temperature. Different experimental temperatures might cause differences in regeneration times.

We observed no morphological differences (with the exception of size and wear on the teeth) between the original and regenerated radulae; therefore, it is highly probable that the regenerated radula is normal in both appearance and function. The fact that all 20 snails resumed feeding and drilled normal boreholes in the oyster shells, implies structural and functional normality in the regenerated radula. The further fact that all 20 snails did not feed until the radular mechanism was completely regenerated, demonstrates that the proboscis and radula are necessary for complete predation. The accessory boring organ is not capable of producing a borehole solely by chemical means (Carriker and Van Zandt, 1972; Webb and Saleuddin, 1977), and the snail could not ingest prey flesh without the radular mechanism.

Unlike *N. lamellosa* that feeds directly through the borehole, *T. haemastoma canaliculata* feeds by inserting its proboscis between the valves of the paralyzed oyster. *Thais haemastoma canaliculata*, therefore, runs a higher risk of proboscetomy during feeding than related species such as *N. lamellosa*. It is possible that an oyster may temporarily recover (especially if it is much larger than the snail) from the toxin and close its valves thus injuring and possibly amputating the drill's proboscis and radula. It is also possible that small crabs might inadvertently enjoy the "delicacies" of exposed proboscis flesh once the valves gape and the crabs enter to feast upon the oyster tissue (Carriker, personal communication). In the laboratory we have observed amputation of a *T. haemastoma canaliculata* proboscis where the oyster (*C. virginica*) had apparently recovered from the toxin and closed its valves thus severing the snail's proboscis. It would be advantageous for this species to have evolved a mechanism for replacing the radula that is essential for its survival. Since *T. haemastoma canaliculata* does not normally extend its proboscis fully even when feeding, if an amputation did occur, part of the radular sac would probably be left behind in the remaining stump, possibly reducing the regeneration time.

Carriker (1975) observed a radular anomaly in a *U. cinerea* in which the central rachidial cusp row was missing after the snail was sacrificed. We discovered a similar anomaly in *T. haemastoma canaliculata* (Figs. 19,20) and were able to keep the snail alive until the radula was completely regenerated. The regenerated radula exhibited the same very reduced central rachidial cusp row. As Carriker (1975) pointed out radular anomalies are rare in the Muricidae. This was the only abnormal radula we observed out of several hundred snails examined over the past three years. Carriker (1975) concluded that the loss of the central cusp row could decrease the feeding efficiency of the snail. We agree with this; however, like Carriker we found that the snail was fairly large (shell length = 61.1 mm) and fed successfully on oysters. Since the regenerated radula was malformed and possessed a reduced central rachidial cusp row like the original radula, we believe this anomaly was genetically induced.

In this investigation all of the animals resumed feeding only after the radula was regenerated, and we believe that the times of radular regeneration and feeding resumption are representative of these processes in nature. Since all of the drills in our experiment recovered completely from the Sevin® and exhibited no observable after effects, we believe that this reinforces the use of Sevin® as an appropriate anesthetic agent for these snails. Sevin® permitted full relaxation of the snails and complete amputation of all of the radular mechanism without any of the mortality experienced by Demoran and Gunter (1956).

Our findings and those of Carriker et al. (1972) illustrate that muricid gastropods possess a remarkably adaptive mechanism for regenerating essential structures which could be extensively damaged or amputated in their natural enivonment. This regenerative mechanism has allowed the snail to take advantage of a potentially risky (to the snail) food source: the American oyster *Crassostrea virginica.*

ACKNOWLEDGMENTS

We would like to express our thanks to Martin Kapper and Debbie Smith for their helpful advice and suggestions during the course of the research. Special thanks are expressed to Tina Fisher for her help in the preparation of the tables and drawings. Appreciation is also extended to Dr. Melbourne R. Carriker for his advice and encouragement.

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SENTENTĬA

REPORT ON COURSES ADVISED FOR GRADUATE STUDENTS IN THE FIELD OF MALACOLOGY

Prepared for the Council of Systematic Malacologists
by
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August 1983

PREFACE

The following report was prepared at the request of the Council of Systematic Malacologists (CSM) and presented to the Council during the 1983 annual meeting of the American Malacological Union in Seattle, Washington. The report was endorsed by the Council as part of the National Plan for Malacology. The report represents the views of CSM, an organization of professional malacologists particularly concerned with collection resource management and use of collections for research.

Malacologists are here defined as persons trained in molluscan systematics or whose interests in the biology of the Mollusca require intensive training in molluscan systematics. Today, such __ologists, whether Ichthyologist or Herpetologist, must be proficient in systematics, ecology and evolution. Those whose career interest are in developmental biology, physiology, ecology, genetics etc. would not call themselves a Malacologist unless their interests were essentially devoted to the Mollusca in some systematic way. Persons specializing in these other fields would require a different array of courses.

REPORT

Many students attending meetings of the American Malacological Union have asked for advice concerning training required to become a Malacologist. Most of these students were undergraduate or beginning graduate students with an interest in systematics, general biology of the Mollusca, or in some special molluscan group.

The courses listed below reflect that today one cannot do state of the art systematic work without understanding the ecology of organisms and without competence in the field of evolution. These interlocking fields require a working knowledge of genetics, mathematics, and statistics.

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The following list was compiled after considering the following criteria: 1) What knowledge is necessary to read and understand the current literature in systematics, ecology and evolution? 2) What skills are needed to conduct first-class research and write synthetic papers on the above subjects for publication in leading peer-review journals? 3) What general knowledge is necessary to address questions raised during job interviews by individuals on search committees? 4) What knowledge would provide the flexibility to apply for different types of jobs if a position in Malacology was not available? Students fully capable in areas based on the courses listed have found employment as invertebrate zoologists, malacologists, ecologists, geneticists, and in allied fields.

While the courses listed below are highly recommended as relevant today and for at least the next decade, proficiency in various topics, e.g. biogeography, can be obtained by extensive reading and self-education; this would suffice instead of taking a course.

Core courses suggested for modern work in Malacology include:

*1. *Invertebrate Zoology:* based on comparative anatomy/embryology.
!2. *Malacology:* fundamentals of classification, systematics, ecology, genetics, physiology, comparative functional anatomy of mollusks.
±3. *Invertebrate Paleontology*
*4. *General Ecology*
!5. *Advanced Ecology:* (community, theoretical, etc.).
!6. *Population Genetics:* (sometimes included in good advanced ecology courses).
!7. *Evolution:* (including systematics, phenetic and cladistic methods).
!8. *Biogeography:* a modern course including historical, dispersal, vicariant, ecological aspects in balance.
*9. *Mathematics* through *Calculus.*
*10. *Biochemistry:* (laboratory course, 1 year).
±11. *Cell physiology:* (physiology, cellular biology).
*12. *Genetics:* (including background molecular genetics, cyto-genetics).
±13. *General Statistics*
!14. *Advanced Statistics:* (through multivariate analysis.) Capabilities with doing computer-mediated analyses are essential.

* best taken during undergraduate education
± take as undergraduate or in graduate school
! take during graduate education

Detailed comparative anatomy is the most underused yet highly valued area of study relative to studies of systematics, evolution, biogeography and adaptive radiation. No phylogenetic construction should be attempted without a data base including detailed anatomical information. Students should be encouraged in this area; anatomical studies should not be considered out of date, they are not. Coupled with sound statistical analyses and computer mediated analyses, comparative anatomical studies are highly desired and relevant. Modern systematics is dependent on detailed anatomical data bases where character-states are derived from an examination of all organ systems.

Modern systematics cannot be adequately undertaken without an understanding of the ecology of the organisms. Adaptive radiation is understood only in terms of adaptation to environmental variables. For example, shell banding may be due to polymorphism where the percentages of different morphs are maintained by predation. Shell shapes are often adaptations to substratum types. Radular differences often relate to different modes of feeding and food types. Reproductive structures may vary due to different reproductive strategies.

Systematists today must be prepared to use multiple data bases to answer questions. Comparative anatomy and ecological data alone may not be sufficient to resolve relationships or allow one to understand pathways of evolution. Severe problems of convergent evolution and genetic change without pronounced morphological change may necessitate use of other methods, e.g. molecular genetics. These biochemical tools have proven valuable during the past two decades for resolving many types of problems unresolved by use of comparative anatomy.

Systematic studies today should not only involve analyses of individual organisms, but also include studies of populations from which the individuals are taken, hence the need for knowledge of population ecology, population genetics, and statistics. The need is to understand variation within and between populations and, if possible, reasons for such variation. One cannot understand the limits of a species without knowledge of variation within and between populations of that species.

THE AMERICAN MALACOLOGICAL UNION
49th ANNUAL MEETING

UNIVERSITY OF WASHINGTON
SEATTLE, WASHINGTON, U.S.A.
AUGUST 7–13, 1983

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ABSTRACTS
MOLLUSCAN NERVOUS SYSTEMS AND BEHAVIOR SYMPOSIUM

Arranged By A. O. Dennis Willows
University of Washington

BEHAVIOR OF GASTROPOD MOLLUSCS. T. E. Audesirk, University of Colorado at Denver.

A brief overview of research in several areas of gastropod behavior was presented, with emphasis on behaviors that lend themselves to analysis at the neuronal level. Gastropods have proven excellent subjects for neuroethology. Their brains are relatively simple, and many have extremely large, brightly pigmented neurons that can be identified as individuals from one preparation to the next. Gastropod behavior tends to be simple and stereotyped, and often consists of rhythmically repeated movements, such as in swimming, crawling, or feeding. General areas of behavior with special applicability to neuroethological research include visually and chemically mediated behavior, locomotion, feeding, and learning.

Research by investigators in each of these areas was described. The general topics covered included the use of visual cues by the marsh periwinkle *Littorina irrorata* to locate stems of marsh grass, and the use of celestial cues to maintain a constant swimming orientation in the opisthobranch *Aplysia brasiliana*. The role of the chemoreceptive structures in both *Aplysia californica* and the terrestrial pulmonate *Achatina fulica* was described. Locomotion in *Aplysia californica* by pedal waves and in the nudibranch *Tritonia* by swimming was reviewed. Feeding behavior in *Tritonia* was also covered.

The neural basis of learning is one of the significant problems of neurobiology and the use of gastropods, especially *Aplysia,* has led to significant contributions in this field. A procedure for classically conditioning the freshwater pulmonate *Lymnaea stagnalis* was described. *Lymnaea* learn to make feeding movements to a non-food odor after it has been paired with food only once, and retain the memory for nearly three weeks.

IDENTIFIABLE NERVE CELLS IN GASTROPOD NEUROBIOLOGY. Gerald Audesirk, Department of Biology, University of Colorado at Denver.

All nerve cells, both in invertebrates and vertebrates, share many fundamental physiological similarities. Nevertheless, individual nerve cells possess unique "personalities" conferred by their morphology, biochemistry, and membrane properties. Nervous systems are therefore not computer-like, in which numerous identical units are connected in complex ways to produce different outputs, but are constellations of more-or-less unique individuals. Behavioral outputs are produced not only by the pattern of interconnection among cells but also by the "personalities" of the individual cells.

The uniqueness of individual nerve cells is most easily seen and utilized in the gastropod brain. Many nerve cells are identifiable by the neurobiologist as unique individuals, on the basis of size, color, position in the brain, axonal morphology, and physiology. In seeking to understand the neural control of a behavior, gastropods offer the potential for determining the exact neurons which influence the behavior, what their role is, and returning for further study to the same neurons in every animal of a given species.

Examples of the use of identified neurons in studying the neural control of behavior include the control of locomotion and plasticity in the decision to feed in the nudibranch *Tritonia diomedea*. Single, identified neurons, one located in each pedal ganglion, have been found to drive cilia on the foot by which *Tritonia* crawls. These neurons send their axons to the foot, where they release the transmitter serotonin, which excites ciliary beating. Another group of neurons in the cerebral ganglia are receptors for food. During escape from predatory starfish, *Tritonia* ignore food stimuli, a process apparently mediated by changes in the responsiveness of these receptors.

***LIMAX* LOGIC: BEHAVIORAL AND NEUROPHYSIOLOGICAL STUDIES OF THE CAPABILITIES OF THE *LIMAX* NERVOUS SYSTEM. Steven J. Wieland,** Department of Biology, Princeton University, New Jersey.

Behavioral experiments have demonstrated higher-order learning processes in the feeding behavior of *Limax maximus*. Neurophysiological studies have revealed the learning ability of the isolated nervous system, and the roles of several transmitters within the feeding network.

A MOLLUSCAN NEUROPEPTIDE ACTS AT MULTIPLE SITES TO MODULATE FEEDING BEHAVIOR IN GASTROPODS. Philip Lloyd, Columbia Medical School, New York, New York.

A neuropeptide (SCP sub-B) recently sequenced from *Aplysia* central nervous system, and neurons which contain this peptide, act centrally to enhance neuronal output from the buccal ganglia, and peripherally to enhance contractile activity of the gut and muscles of the buccal mass.

ABSTRACTS
MOLLUSCAN EXTINCTIONS IN THE GEOLOGIC PAST AND THE PRESENT TIME

Arranged by Geerat J. Vermeij
University of Maryland

ON THE CRETACEOUS EXTINCTION OF THE AMMONITE CEPHALOPODS. Peter Ward, Department of Geology, University of California, Davis.

The ammonites were the most diverse group of cephalopods known from the fossil record. After a long evolutionary history, they underwent complete extinction at the end of the Cretaceous period. This extinction, however, was preceded by changes in shell morphology which can be interpreted to imply major habitat change, and possibly change in mode of life prior to the extinction event itself.

FAUNAL REPLACEMENT AND CAUSES OF POST-MIOCENE EXTINCTION OF PELECYPODS IN THE CHESAPEAKE BAY REGION OF MARYLAND. Brett W. Kent and **Geerat J. Vermeij,** Department of Zoology, University of Maryland, College Park.

Only 28 of 72 subgenera (39%) of epifaunal and sand- and mud-burrowing pelecypods present in latest Miocene time in the Chesapeake Bay region of Maryland are living today in shallow waters of the Virginian Province (Cape Cod to Cape Hatteras). There are 12 globally extinct taxa which appear to have been endemic to the Chesapeake region. Of the 32 subgenera which have become locally extinct, all are known south of Cape Hatteras, and only one has a broad distribution extending both north of Cape Cod and south of Cape Hatteras. The modern Virginian shallow-water fauna of epifaunal and burrowing bivalves consists of 55 subgenera, of which 27 (49%) are not known as fossils. Both among taxa not known as fossils and among taxa surviving from the Miocene, broad latitudinal distributions are common (22 subgenera, 40% of modern fauna), and a substantial number (12 taxa, 22%) is characterized by a northern distribution extending from within the Virginian Province to north of Cape Cod. These distributional data are consistent with those of Petuch (1983) for gastropods. They suggest strongly that the Late Miocene climate of Maryland was both warmer and less extreme in temperature range than it is today. Moreover, substantial immigration from the north has occurred, resulting in a partial faunal replacement and in a faunal mixture consisting of surviving local taxa with a southern or latitudinally broad distribution and of an introduced northern fraction. Stanley and Campbell's (1981) hypothesis that the chief cause of extinction in the Western Atlantic was a shift in climate is supported by our data from Maryland.

DIFFERENTIAL EXTINCTION IN TROPICAL AMERICAN MOLLUSCS: ENDEMISM, SHELL ARCHITECTURE, AND THE PANAMA LAND BRIDGE. Geerat J. Vermeij and **Edward J. Petuch,** Department of Zoology, University of Maryland, College Park.

The uplift of the Central American isthmus during the Pliocene triggered a substantial impoverishment in the biota of tropical America. We tabulated all Pliocene supraspecific taxa and their living descendants in 17 families and superfamilies of molluscs for each of three marine biogeographical regions: (1) the Caloosahatchian Province, centered in Florida; (2) the Atlantic Gatunian region, comprising the modern tropical Atlantic; and (3) the Pacific Gatunian region, corresponding to the modern tropical Eastern Pacific. Extinction affected gastropods to a greater extent in the Caloosahatchian (36%) and Atlantic Gatunian regions (36%) than in the Pacific Gatunian area (15%). In all regions, endemic taxa suffered more than 50% extinction. Because the Atlantic faunas were substantially richer in endemics than was the Eastern Pacific, part of the interoceanic difference in the impact of extinction is attributable to the high susceptibility of narrowly distributed taxa to extinction. Patterns of extinction in bivalves were similar to those in gastropods.

The tendency for hard-bottom gastropods to be somewhat more resistant to extinction than were soft-bottom taxa is shown to be partly the result of an artifact of geographical range, there being relatively few endemic taxa among hard-bottom gastropods. Hard-bottom taxa with a narrow or thick-lipped aperture were more susceptible to extinction in the Atlantic than were their wide-apertured counterparts. This pattern, which is not an artifact of geographical range, resulted in a post-Pliocene decline in the incidence of apertural protective devices among hard-bottom Atlantic gastropods while the incidence in the Eastern Pacific remained constant.

THE TAXONOMIC STRUCTURE OF SHALLOW-WATER MARINE FAUNAS: IMPLICATIONS FOR PHANEROZOIC EXTINCTIONS. David Jablonski, Department of Ecology and Evolutionary Biology and **Karl W. Flessa,** Department of Geosciences, University of Arizona, Tucson.

The taxonomic and biogeographic structure of Recent shallow-marine faunas provides a means of evaluating the causes and magnitudes of extinctions in the fossil record. We assembled data on the distribution of families of marine gastropods, bivalves, echinoderms, and scleractinian corals, and on the number of species within families in gastropod, bivalve, and echinoid faunas. The 22 oceanic islands for which we collected data harbor a very large proportion (87%) of the global, shallow-water marine fauna, and 78% of the families are on two or more of those islands. Even if eustatic lowering of sea level completely eliminated the continental shelf faunas (itself an unlikely prospect), oceanic islands would provide a safe haven for representatives of the great majority of today's shallow-marine benthic families; this indicates that the effects of areal reduction alone are insufficient to explain extensive familial extinction during the mass extinctions associated with regression.

Continental shelf bivalve and echinoid faunas have significantly more species per family than island bivalve and echinoid faunas (a proportion of 1.5:1 and 1.3:1, respectively), though gastropod faunas show no such difference. Gastropod faunas display persistently higher species-family ratios than bivalve faunas, and echinoid faunas have the lowest ratios of the three classes. Species-family ratios are diversity-dependent, so that island-continental and class-to-class differences in species-family ratios appear to be a consequence of differing species richness among the faunas and classes.

The fossil record suggests that species richness within clades may not be an adequate measure of resistance to mass extinction. Tropical clades appear to suffer disproportionately during times of mass extinction, and in general species-rich clades are not better represented among survivors than species-poor clades. The linkage between speciation and extinction rates generates species-rich but evolutionarily volatile clades. Species richness within clades may, however, contribute to a clade's resistance to background extinction. That different factors contribute to extinction-resistance during times of mass vs. background extinctions suggest that macroevolutionary processes during those times are qualitatively as well as quantitatively different.

AVIAN MOLLUSCIVORES MINISYMPOSIUM

Arranged by David R. Lindberg
University of California

DESIGNER LIMPETS AND THEIR AVIAN CONSUMERS. Fred Sorenson, Moss Landing Marine Laboratories, California.

The limpet *Collisella pelta* has different shapes and forms on different substrata. Movement between substrata results in color patterns that make them conspicuous to avian predators. Transitional forms show up in higher proportions in Black Oystercatcher (*Haematopus bachmani*) middens than in the surrounding environment.

INTERTIDAL COMMUNITY STRUCTURE IN CENTRAL AND SOUTHERN CALIFORNIA: THE INTERACTION BETWEEN HUMAN DISTURBANCE, BIRD PREDATION, AND LIMPET TERRITORALITY. David R. Lindberg, James A. Estes, and **Kenneth I. Warheit,** Center for Coastal Marine Studies, University of California at Santa Cruz.

The presence or absence of the territorial limpet *Lottia gigantea* determines species diversity and abundances in the high and mid intertidal zones. The abundance of *L. gigantea*, in turn, is determined by the abundance of oystercatchers and humans. Humans also determine the abundance of oystercatchers.

ABSTRACTS
SUPPORT SERVICES IN MALACOLOGY

A PROPOSED GENERALIZED MOLLUSCAN SHELL GROWTH MODEL: GASTROPOD MORPHOLOGY AND CONSTRUCTIONAL PATTERNS. Matthew J. James, Department of Paleontology, University of California, Berkeley.

The great diversity of molluscan shell form can be classified and analyzed using components of the proposed shell growth model. This is a descriptive model, not a mathematical model or computer simulation, and is therefore based on empirical observations. Using gastropods as examples of complex constructional patterns, the model aids identification of temporal and spatial components of alteration in shell structure, ornamentation, and architecture. Two principal modes of calcium carbonate manipulation (deposition and resorption) are modified by four fundamental factors: 1) spatial variation (uniform or localized), 2) temporal variation (continuous or periodic), 3) positional variation (interior or exterior), and 4) rate variation (constant or enhanced). Utilization of the model is facilitated by two 16-way contingency diagrams (containing factor permutations) that aid identification of either depositional or resorptive events. The shape, surface area, and number of secretory cells along the mantle edge are important features influencing shell growth. Regions of mantle tissue responsible for shell fabric manipulation can be thought of as essentially receiving temporally variable "on-off" commands that are environmentally modulated or intrinsically coded by the organism. Calcium carbonate accumulations are due to changes in depositional rate and/or changes in mantle tissue advancement rate. Particular features of shell ornamentation, such as a spine, spiral cord, or varix, can be conceptually analyzed in the framework of depositional or resorptive modification of spatial, temporal, positional, and rate components of growth. Biologically plausible but physiologically costly methods of creating shell ornamentation are identified. Interior architectural reorganization by allocation of carbonate resources to other shell regions is contrasted with "background" shell deposition. Considering a series of controlling factors for calcium carbonate manipulation (such as phylogeny or environment), the growth histories of fossil gastropods (or other molluscan classes) can be described and interpreted for paleobiological significance. The implications of this model for evolutionary malacology lie in a better understanding of functionally and taxonomically important components of shell growth.

COMPUTERIZATION OF TAXONOMIC CATALOGUES.

Alan J. Kohn, Department of Zoology, University of Washington, Seattle.

Indispensable to the practicing taxonomist, catalogues of available scientific names have previously been published as reports in the professional literature. Recent advances in microcomputer technology permit a more flexible method of producing catalogues with several advantages over traditional publication: 1) Information storage is more efficient and flexible. New taxa are easily entered, errors are easily corrected, and the computer sorts entries to the cataloguers desired format. 2) Valuable journal space is not occupied by material of interest to relatively few workers. Print-outs can be inexpensively distributed to users, and the professional journal need only announce availability of the catalogue. 3) The catalogue is always up to date, as the latest information entered is incorporated into the pre-existing catalogue. Each recipient receives the latest available, dated printout.

ADMINISTERING A SHELL CLUB SCHOLARSHIP PROGRAM.

Wesley Thorsson and **Stuart Lillico.** Hawaiian Malacological Society, Honolulu, Hawaii.

The Hawaiian Malacological Society is a nonprofit educational organization. For its first 30 years this educational factor was limited almost entirely to upgrading *Hawaiian Shell News* as a vehicle for reporting and discussing progress in malacology. This function is still paramount but since about 1972 the Society has been increasingly involved in giving direct financial assistance to students of malacology.

The Society in the past decade has committed close to $20,000 in prizes, awards and grants.

Two major obstacles have had to be overcome. The first, and in many ways the most difficult, was in reaching agreement that this was a proper use for the Society's assets. There is still some resistance. The second continues to be the problem of making the program known.

Since 1978 the Society has had four award programs in effect. These are, first, annual awards to high school and grade school participants in the Hawaii State Science and Engineering Fair; second, the E. R. Cross Awards to young exhibitors in the biennial HMS Shell Shows; and, third, grants to undergraduate and graduate students engaged in programs leading to involvement in malacology. The fourth assists the B. P. Bishop Museum.

Our major award program, which assists advanced students of malacology, has been financed primarily by proceeds from HMS shell auctions and a portion of the interest earned on HMS assets. To date these awards to college students or their equivalent total $16,993.

The Society's fourth and newest program, set up two years ago, is designed to assist Hawaii's B. P. Bishop Museum. Interest from approximately $16,000 of the Society's assets was earmarked for the museum's benefit, and early in 1983 $1800 was voted as partial funding for an individual to assist in clearing the backlog of curatorial tasks in the Malacology Department of the Museum.

Our scholarships normally support projects that will contribute to malacological knowledge in general and to the ecological and conservation goals of the Society in particular, as well as contributing to the candidate's academic progress. Possibly most significant has been the number of projects in mariculture.

One ambition remains unfullfilled. We would like eventually to see a study center established for the benefit of amateur malacologists—preferably in Honolulu, of course. We believe such a center would serve as a significant bridge between serious amateur shell collecting and professional malacology.

ABSTRACTS
POSTER SESSION

THE ULTRASTRUCTURE OF SMOOTH MUSCLE CELLS FROM THE ANTERIOR ADDUCTOR MUSCLE OF *LASMIGONA COSTATA* (RAFINESQUE, 1820) (MOLLUSCA: BIVALVIA: UNIONIDAE). Michael A. Hoggarth, The Ohio State University Museum of Zoology, Columbus.

Specimens of *Lasmigona costata* (Rafinesque, 1820) were collected on 16 October 1982 from Big Darby Creek in Pickaway County, Ohio. Anterior adductor muscle from this species was excised and prepared for examination in an electron microscope. Smooth muscle cells with paramyosin-containing thick filaments were observed. These filaments had a diameter between 650 nm to 950 nm. Some filaments were found in oblique orientation to the predominant direction of myofilaments in the cells. This is a character shared by the genus *Anodonta* and in fact the smooth muscle cells of the adductor muscles of *Anodonta* and *Lasmigona* were found to be similar. Also contained within the smooth muscle cells of *L. costata* is a single central nucleus per cell, peripheral mitochondria and an extensive sarcoplasmic reticulum. The cells are surrounded by a sarcolemma and nerve endings containing dense-core vesicles were found within the endomysium.

MOVING THE CANADIAN NATIONAL MOLLUSC COLLECTION AND A TOUR OF THE NEW FACILITIES. Jane M. Topping, Mollusc Unit, IZD, NMNS, NMC, Ottawa, Ontario, Canada.

In July 1967 the Canadian National Mollusc Collection was moved from the Victoria Memorial Museum Building to temporary quarters in the Beamish Building. These accommodations proved very inadequate for both collection storage and working conditions as the building had been constructed as a warehouse. We were housed there until November 1982 at which time we undertook to move to yet another temporary location. The new accommodations provide excellent facilities and should prove more than adequate until such time as the proposed central complex for all of the Museum of Natural Sciences is constructed.

The Mollusc Unit is now located at 2379 Holly Lane in the SE end of the city close to Ottawa International Airport. An invitation is extended to researchers to visit. For more information please contact:

Mollusc Unit, Invertebrate Zoology Division
Nat. Mus. Nat. Sci., Nat. Mus. Can.
2379 Holly Lane
Ottawa, Ontario
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Area Code (613) 998-9262

SHELL SHAPE AND SEXUAL DIMORPHISM IN *AFORIA CIRCINATA* (PROSOBRANCHIA: TURRIDAE). Ronald Shimek, Bamfield Marine Station, British Columbia, Canada.

Mature females of *Aforia circinata* develop a distinct canal-like notch on the anterior edge of the outer shell lip. This notch is not found in immature animals of either sex or mature males. Sexual maturity appears to occur at lengths of about 70 mm, and all females over 72 mm long have the notch. Smaller females may have a low ridge, with similar ridges found on a few mature males, that appears to be an ontogenetic precursor of the notch. Similar notches are seen in a few other deep water turrid species, and may represent common solutions to some reproductive stress, possibly encountered during oviposition, of the females.

LINNAEUS'S ARRANGEMENT OF SHELLS. A. J. Cain, Zoology Department, University of Liverpool, United Kingdom.

It is usually said that the last class, *Vermes,* in Linnaeus's classification of animals (*Systema Naturae,* 10th edition, 1758) is purely artificial, a mere rag-bag of forms he could not place elsewhere. An examination of the order Testacea shows that, on the contrary, the genera and species are carefully arranged in a series, connecting to the previous order (Mollusca) and the succeeding one (Lithophyta). We know that Linnaeus insisted that genera must be natural; he may well have thought of the whole series as natural, as well as a great convenience in identification. It is not certain whether he regarded it as the Ladder of Nature, or as the product of hybridization (or, of course, both).

ABSTRACTS
CONTRIBUTED PAPERS

KIDNEY FUNCTION IN GIANT CLAMS. R. G. B. Reid, Department of Biology, University of Victoria, Victoria, British Columbia.

The hypertrophied kidneys of giant clams have a digestive function, and can process zooxanthellae and store toxic and unusable components in nephroliths.

A TAXONOMIC REVISION OF THE CRASSATELLINAE OF THE EASTERN PACIFIC, WITH SOME COMMENTS ON THE BIOGEOGRAPHY OF THE PANAMA CONNECTION. Eugene Coan, Department of Zoology, California Academy of Sciences, Golden Gate Park, San Francisco.

The three Recent eastern Pacific species of the Crassatellinae belong in *Eucrassatella* Iredale, 1924. *Hybolophus* Stewart, 1930, is regarded as a synonym of this genus, as is the recently proposed but unavailable *Eucrassinella* Cruz, 1980. The rare *E. fluctuata* (Carpenter, 1864) occurs off the Channel Islands of southern California at a mean depth of 88 m; a synonym is *Crassatellites lomitensis* Oldroyd, 1924. *Crassatella marginata* Keep, 1887, "*ex* Carpenter MS," which has been synonymized with *E. fluctuata,* is instead based on specimens of the bernardinid genus *Halodakra,* perhaps *H. salmonea* (Carpenter, 1864). *Eucrassatella gibbosa* (Sowerby, 1832) occurs from the Gulf of California to Peru at a mean depth of 32 m. Added to its synonymy are *Eucrassatella (Hybolophus) gibbosa tucilla* Olsson, 1932; and *Eucrassatella manabiensis* and *E. aequitorialis* Cruz, 1980. *Crassatella corbuloides* Reeve, 1842, which has been synonymized with *E. gibbosa,* is instead an Australian taxon. The Venezuelan *Eucrassatella antillarum* (Reeve, 1842) is synonymized with the eastern Pacific E. digueti (Lamy, 1917). In the eastern Pacific this species occurs at a mean depth of 45 m from the Gulf of California to Ecuador. Newly added to its synonymy is *Crassatella laevis* A. Adams, 1854, from the Caribbean.

There has been an overrecognition of full, cognate species between the Panamic and Caribbean faunal provinces. Increased consideration should be given to the use of subspecies or describing the morphological differences between populations without naming them.

DESCRIPTION OF FIVE NEW SPECIES OF HAWAIIAN EULIMIDAE. Anders Warén, University of Goteborg, Sweden, **Beatrice L. Burch** and **Thomas A. Burch,** Kailua, Hawaii.

Five new species of Eulimidae obtained from echinoids collected by scuba or dredging from 15 to 470 meters off Oahu, Hawaii are described briefly. Since the article naming the species has not been published, specific names will not be used.

A species of *Trochostylifer* was found in galls on the heavy dorsal spines of *Chondrocidaris gigantea* at depths of 15 to 25 meters. A second species of *Trochostylifer* was found in the galls on the test of the closely related echinoid, *Prionocidaris hawaiiensis* from a depth of 72 meters.

Two species that have been placed provisionally in the genus *Vitreolina* were found on the same two species of echinoids.

The fifth species of eulimid is in the genus *Pelseneeria,* which was found on *Aspidodiadema hawaiiensis* dredged from 470 meters off Honolulu.

LARVAL WASHOFF: EULIMID INFESTATION RATES AROUND AN OCEANIC ISLAND. Gustav Paulay, University of Washington, Seattle.

Oceanic islands in a steady current generated by trade winds face a loss of pelagic larvae of marine invertebrates carried off by the current. Although eddies, longshore currents, and lagoons may facilitate larval retention, there is still an expected loss as well as net transport of larvae from the windward to the leeward side of an island. To test this prediction, I investigated infestation rates by *Melanella* sp., a eulimid prosobranch inhabiting the body wall of *Stichopus chloronotus,* an aspidochirote holothurian around Rarotonga, Cook Islands. Eight sites around the island's periphery were examined, seven on the narrow (20–700 m wide) fringing reef and one on the outer reef slope. *Stichopus* is almost entirely restricted to the fringing reef. An endoparasite is the best adult system for this type of study, as its habitat (the host) is easily ascertained, and internal parasites are least affected by external stresses. Infestation rates change from 0.05 parasite/host on the East (windward) side through 0.46 on the North, to 0.84 on the West (leeward) side of the fringing reef. Three alternative hypotheses, 1) selective mortality, 2) association with reef exposure, and 3) dependence on host size, are rejected. A fourth, greater ease of host infection on the leeward side, cannot at present be rejected, as the host is more crowded, and smaller there. However, this latter observation is also consistent with larval washoff affecting the host population.

HOW *CYPHOMA* GET THEIR SPOTS: DIET MIXING. C. Drew Harvell, Department of Zoology, University of Washington, Seattle.

Cyphoma gibbosum is a ubiquitous, tropical cowrie that feeds on gorgonian colonies inhabiting shallow Caribbean reefs. Adults are brightly colored and juveniles are cryptic. Adult coloration is due to an unusual color pattern incorporated into a retractable mantle: hollow black spots outlined against a contrasting orange or yellow background. Juvenile coloration is similar, but the spots are muted and blend with the prey colony. Thus juveniles on both light and dark colonies are cryptic against their prey. The mechanism of the color change is unknown, but may be due to chromatophores or differential pigment uptake from the prey.

The juvenile-adult color shift coincides with an ontogenetic shift in foraging behavior; juveniles remain on single colonies, but adults move regularly between colonies. Juveniles therefore behave as extreme trophic specialists and adults as trophic generalists. The spots on the mantle may become more clearly outlined when *Cyphoma* develop the "diet mixing" behavior of an adult and ingest several species of gorgonian during a brief time interval. This supports the notion that coloration is affected by ingestion of prey pigments.

The association of trophic specialization and cryptic coloration described for juvenile *Cyphoma* occurs in other trophic specialists. Trophic specialization may be a precondition favoring the evolution of cryptic coloration in many carnivorous molluscs and other taxa. Exceptions to the association of trophic specialization and cryptic coloration within the order Nudibranchia are common among species that feed upon prey possessing toxic chemicals; these species appear to be warningly colored and may incorporate toxins from their prey.

THE *CALLIOSTOMA PULCHRUM* SPECIES COMPLEX IN THE NORTHERN WESTERN ATLANTIC. James F. Quinn, Jr., Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg.

Apparent intergrades in shell morphologies between *Calliostoma pulchrum* (C. B. Adams, 1850) and *C. roseolum* Dall, 1881, prompted a reexamination of the *C. pulchrum* species complex within the northern Western Atlantic. Five distinct forms were evaluated: *C. pulchrum* (Caribbean), *C. roseolum* (southeastern U.S.), *C. apicinum* Dall, 1881, *roseolum* (Barbados), *C. veliei* Pilsbry, 1900 (southeastern U.S.), and an unnamed form (Texas).

UPDATE ON MOLLUSKS WITH INDO-PACIFIC FAUNAL AFFINITIES IN THE TROPICAL EASTERN PACIFIC II. Donald R. Shasky, Redlands, California.

Cocos Island, Costa Rica, 300 miles SSW of Puentarenas C.R., is the largest uninhabited island in the world. It has a land mass of 20 square miles. Its annual rainfall is 22 feet.

Recent diving has produced specimens of the following Indo-Pacific mollusks previously unreported in the Panamic Province:

Viriola abbotti (Baker and Spicer, 1935)
Scalenostoma subulata (Broderip, 1832)
Cypraea talpa (Linnaeus, 1758)
Cypraea nsp. Burgess, 1983
Charonia tritonis (Linnaeus, 1758)
Favartia garretti (Pease, 1869)
Persicula pulchella (Kiener, 1834)
Spondylus nicobaricus, Schreiber, 1793

The *Cypraea* nsp. Burgess, 1983, is in press. It ranges throughout much of the Indo-Pacific.

PALEOECOLOGY AND MOLLUSCAN FAUNA OF THE ESMERALDAS FORMATION OF ECUADOR. Gary Rosenberg, Mollusk Department, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

A collection of mollusks from the Esmeraldas Formation containing 165 species was analysed. About 100 of these species are new records for the Esmeraldas, increasing the number of species known in the fauna to about 260. Most of the new records are of species a centimeter or less in length.

Ecological comparisons of Recent taxa related to the fossil species show that the fauna lived offshore on the continental shelf on a mud substratum in water 50 to 100 meters deep.

Studies of the planktonic foraminiferal fauna restrict the age of the Esmeraldas to 3.6 to 3.2 myBP, corresponding to early Late Pliocene. The Esmeraldas was previously assigned to the late Miocene or early Pliocene by workers using the Lyellian system of dating, as almost 80 percent of the species in the fauna are extinct. The Lyellian system gives dates that are too old as it fails to take into account the increased extinction rates caused by the uplift of the Panamanian landbridge, and by glacially controlled fluctuations in sea level.

TERTIARY MOLLUSCAN DISTRIBUTIONS FROM BAJA CALIFORNIA SUR, MEXICO. Judith Terry Smith, U.S. Geological Survey, Menlo Park, California.

Molluscan data provide valuable information on the geologic history of the Gulf of California and the paleogeographic reconstruction of Baja California. Marine waters first entered the southern part of the Gulf about 5 m.y. ago, and the fauna has been the same since the middle Pliocene. The Baja California peninsula is composed of a mosaic of geologic terranes, each with a distinctive stratigraphic and tectonic history. Some terranes (e.g., the Viscaino peninsula) may have traveled far; others are autochthonous within the Pacific-Panamic faunal province. Fossiliferous strata that overlie adjacent terranes constrain the time they came together. First occurrences of exotic taxa, provincial extinctions, and phylogenetic sequences of index species are used to date and correlate formations in the Viscaino peninsula, the Magdalena Plain, the Purisima area, the Cabo Trough, and the Gulf of California.

Newly collected fossils indicate that major revisions are necessary in the age assignments of earlier literature. Miocene mollusks typical of a mangrove environment were collected in the Cabo Trough from the basal part of the Trinidad Formation, which was previously regarded as a deep-water deposit. Miocene taxa from the type section of the "Pliocene" Salada Formation are correlative with the middle Miocene Gatun Formation of Panama. A Miocene strandline is preserved near Todos Santos, where nonmarine vertebrate fossils overlie beach deposits containing *Vasum* sp. cf. *V. pufferi, Turritella abrupta,* and *Cancellaria (Pyruclia)* sp. cf. *C. (P.) diadela.* Caribphile *Melongena melongena consors, Cymia cheloma,* and *Turritella* 5 spp. document that Tertiary Caribbean Province index fossils of middle Miocene age occur in Baja California. Caribbean species also occur near La Purisima in the Miocene Isidro Formation with *Rapana imperialis,* a cognate of the Holocene *R. bezoar* from the western Pacific and a descendant of *R. vaquerosensis* from the Oligocene of California. Systematic treatment is complicated for these taxa, many of which have different western Atlantic, western Mexican, Californian, and South American names.

An important question is: Did Tertiary Caribbean assemblages range northward to Baja California, or have some been transported as parts of tectonic terranes? Oceanic currents, possibly related to unusually strong El Niño effects, have been considered a likely vehicle for distribution, but many taxa (including *Melongena* and *Turritella*) undergo direct development or have a very short planktotrophic larval stage. Dispersal mechanisms must be determined for the whole Tertiary Caribbean assemblage and geographic range considered within a tectonostratigraphic context.

GALAPAGOS ISLANDS MARINE INVERTEBRATE EVOLUTION: A NEW PATTERN EMERGES.

Matthew J. James and **Patrick F. Fields,** Department of Paleontology, University of California, Berkeley.

Consideration of some of the inherent biological differences between the well-known terrestrial biota and the marine invertebrate fauna of the Galapagos Islands has resulted in an alternative interpretation of evolutionary processes in the islands. Rates of evolution frequently associated with the Galapagos terrestrial biota are not substantiated by the marine invertebrate fauna. Contrasting marine invertebrate with terrestrial organisms highlights some fundamental differences having important evolutionary implications. Endemism at the specific and higher taxonomic levels is observed to be lower in the marine invertebrate fauna than in the terrestrial biota. The ability of many members of the former to disperse propagules (and thus genetic material) between populations, as compared to the less likely exchange between mainland and island terrestrial populations supports this idea. Consequently, marine invertebrates experience a lower degree of isolation and reduced frequency of endemicity at all taxonomic levels. Decreasing degrees of taxonomic difference are seen when comparing mainland to archipelago, inter-island, and intra-island terrestrial populations. Such differences usually exist for marine organisms only in the former comparison. Inter-island and intra-island population differences are obscured and/or supressed in the marine realm by difficulty in bathymetrically defining an island and by the ease of propagule exchange, discussed above. Differences in intrinsic rates of evolutionary change between vertebrate and invertebrate organisms could contribute additional reasons for the observed terrestrial and marine patterns. Evolutionary differences are reflected in the taxonomic hierarchy applied to Galapagos organisms. However, fossil evidence in the islands favors reconsideration of the taxonomic relationships of many marine organisms. Isolation, adaptive radiation, and speciation (evolutionary divergence) do not obtain as a viable evolutionary scenario for many marine invertebrate organisms in the Galapagos. In terms of Darwin's evolutionary scenario, terrestrial organisms represent the paradigm and marine organisms represent the paradox.

Note: A more detailed version of these ideas will appear as part of a symposium volume on evolution in the Galapagos Islands in the *Biol. Jour. Linn. Soc.* 21(1) Jan./Feb. 1984.

NAIADES OF THE CURRENT RIVER BASIN, MISSOURI.

Alan C. Buchanan, Missouri Department of Conservation, Columbia.

Thirty-two species of naiades were found at 33 sites in the Current and Jacks Fork Rivers in southern Missouri and northern Arkansas. Twenty-nine species were found in Current River, including the endangered *Lampsilis orbiculata. Lampsilis reeviana* (40.3%), *Ptychobranchus occidentalis* (19.6%), *Cyclonaias tuberculata* (11.1%), *Pleurobema coccineum* (8.4%), *Fusconaia ozarkensis* (5.5%), and *Villosa iris iris* (4.1%) comprised 89% of the living naiades found in Current River. Fifteen species of naiades were found in Jacks Fork River, where *Lampsilis reeviana* (34.5%), *Ptychobranchus occidentalis* (30.8%), *Villosa iris iris* (11.4%), and *Fusconaia ozarkensis* (10.2%) comprised 86.9% of the living naiades found. Cold spring inflows reduced naiad abundance and species diversity both locally and over the length of Current and Jacks Fork Rivers.

A SURVEY OF THE FRESHWATER MUSSELS OF THE KANAWHA RIVER, WEST VIRGINIA.

Ralph W. Taylor, Marshall University, Huntington, West Virginia.

A reconnaissance of the Kanawha River from head to mouth produced data on 27 species of freshwater mussels plus the Asian clam. The majority of specimens were found in a stretch of river, approximately five miles long, immediately below Kanawha Falls. Only six species of mussels were found above the falls.

The large population below Kanawha Falls is healthy and in no apparent danger at this time. It is located above slackwater and well above the navigation pool. Increased use of the Kanawha by barge traffic should have no effect on this population.

The lower 75 miles are presumed to be devoid of bivalve life with the exception of the Asian clam. Good populations of this clam were found sporadically along the reach of the river.

Two species of freshwater mussels, which are currently listed by the U.S.F.W.S. as endangered or threatened, have been reported in recent times as occurring in the Kanawha River headwaters. Only one of the two species, *Lampsilis orbiculata,* was found during this study. *Epioblasma t. torulosa* was not found and can be presumed to no longer survive in this drainage. *Lampsilis orbiculata* was found only in the stretch between Kanawha Falls and the head of slackwater. A fairly good-sized healthy population exists at this locality.

Additional Species Found

Anodonta imbecillis Say, 1829
Anodonta g. grandis Say, 1829
Strophitus u. undulatus (Say, 1817)
Simpsonaias ambigua (Say, 1825)
Lasmigona costata (Rafinesque, 1820)
Lasmigona subviridis (Conrad, 1835)
Megalonaias nervosa (Rafinesque, 1820)
Tritogonia verrucosa (Rafinesque, 1820)
Quadrula pustulosa pustulosa (Lea, 1831)
Amblema p. plicata (Say, 1817)
Fusconaia m. maculata (Rafinesque, 1820)
Cyclonaias tuberculata (Rafinesque, 1820)
Pleurobema sintoxia (Rafinesque, 1820)
Pleurobema cordatum (Rafinesque, 1820)
Pleurobema rubrum (Rafinesque, 1820)
Elliptio c. crassidens (Lamarck, 1819)
Elliptio dilatata (Rafinesque, 1820)
Ptychobranchus fasciolaris (Rafinesque, 1820)
Plethobasus cyphyus (Rafinesque, 1820)
Obliquaria reflexa Rafinesque, 1820
Cyprogenia stegaria (Rafinesque, 1820)
Actinonaias l. carinata (Barnes, 1823)
Ellipsaria lineolata (Rafinesque, 1820)
Obovaria subrotunda (Rafinesque, 1820)
Truncilla truncata Rafinesque, 1820
Leptodea fragilis (Rafinesque, 1820)
Potamilus alatus (Say, 1817)
Ligumia recta (Lamarck, 1819)
Villosa i. iris (Lea, 1829)
Lampsilis r. luteola (Lamarck, 1819)
Lampsilis ventricosa (Barnes, 1823)
Lampsilis ovata (Say, 1817)
Lampsilis fasciola Rafinesque, 1820

THE DISTRIBUTION OF UNIONIDAE IN THE CALCASIEU RIVER IN SOUTHWESTERN LOUISIANA (MOLLUSCA: BIVALVIA: UNIONOIDA). David H. Stansbery and **Michael A. Hoggarth,** The Ohio State University Museum of Zoology, Columbus.

A series of eleven study sites on the main stem of the Calcasieu River revealed a fauna of twenty-two species of unionids, two species of *Sphaerium* and one species of *Corbicula* distributed over the nine uppermost sites. The lower two sites yielded six species of marine or estuarine bivalves and no freshwater species.

FRESHWATER BIVALVES OF THE LOWER RIO GRANDE SYSTEM, UNITED STATES AND MEXICO. Raymond W. Neck, Texas Parks and Wildlife Department, Austin, Texas, and **Art L. Metcalf,** Department of Biological Sciences, University of Texas at El Paso.

The Rio Grande system is one of the longer river systems of North America. Few field studies have covered this system because of its distance from centers of malacological study and the paucity of the bivalve fauna. This study was restricted to the lower Rio Grande from Falcon Reservoir to the Gulf of Mexico.

Species known from this lower portion of the Rio Grande are as follows: *Anodonta imbecillis henryiana* (Lea, 1857); *Anodonta grandis* (Say, 1829); *Uniomerus tetralasmus manubius* (Gould, 1855); *Megalonaias gigantea* (Barnes, 1823); *Quadrula apiculata* (Say, 1829); *Popenaias popei* (Lea, 1857); *Cyrtonaias tampicoensis berlandieri* (Lea 1857); *Toxolasma parvus* (Barnes, 1823); *Lampsilis teres* (Rafinesque, 1820); *Disconaias salinasensis* (Simpson, 1908); and *Corbicula fluminea* (Müller, 1774).

Most abundant species are *C. t. berlandieri, A. imbecillis* and *C. fluminea. U. t. manubius* has apparently not been collected since the original lot was procured from northern Mexico. *C. fluminea* may be locally abundant in faster-moving water in the Rio Grande and wave-washed shores of Falcon Reservoir. Several species *(M. gigantea, P. popei* and *D. salinasensis)* are known only from the Rio Grande proper.

Human impact upon the bivalve fauna of the lower Rio Grande has been varied. Most important is control of floods via a system of levees to contain high water flows, draining of certain resacas (abandoned river channels), agricultural and urban runoff, construction of Falcon Reservoir, and a button industry utilizing *C. t. berlandieri.*

Native bivalves of the lower Rio Grande are derived from two zoogeographical realms: Mississippian or Central Basin to the northeast, and the Mexican Gulf Coast to the south. Relatively few species have their affinity to the south. Close approach of low-elevation mountains to the Mexican coast has apparently restricted coastal plain stream migration. Therefore, few southern species occur in the lower Rio Grande.

ORIENTATION OF *LAMPSILIS RADIATA LUTEOLA* (LAM.) (BIVALVIA: UNIONIDAE) IN THE EAST FORK OF THE LITTLE SANDY RIVER, BOYD COUNTY, KENTUCKY. Karen J. Horn, Department of Biological Sciences, Marshall University, Huntington, West Virginia.

The orientation of *Lampsilis r. luteola* (Lam., 1819) was measured at three locations in the East Fork of the Little Sandy River, Boyd County, Kentucky. A mussel pointing directly upstream was assigned an angle of zero and one pointing downstream, an angle of 180°. The angular frequency distribution was fit to a Poisson distribution as a test for randomness. Mussels were randomly oriented at only one location. The other locations and the combined data exhibited a clumped distribution. In addition, six morphometric characters were examined for their relationship to the angle of orientation using a cluster correlation analysis. Sex and obesity were positively correlated with the angle of orientation. Females tended to orient themselves in the downstream direction. Males preferred to siphon upstream.

AN ANALYSIS OF NAIAD CHROMOSOMAL MORPHOLOGY (BIVALVIA: UNIONACEA). John J. Jenkinson, Ohio

State University and Tennessee Valley Authority, Knoxville, Tennessee.

In 1977, Jenkinson (*AMU Bulletin* for 1976:16–17) reported a diploid chromosome number of 38 for 15 North American naiad species. That research eventually included five or more counts from 41 North American naiad species, all of which had 38 as the modal diploid chromosome number. In addition, 26 other species-level taxa were represented by between one and four counted chromosome spreads, again with 38 the apparent diploid number. The constant 38 diploid number in North American species is identical to published reports for three European unionids (Van Griethuysen, Kiavta, and Butot. 1969. *Basteria* 33:51–56) and one Japanese margaritiferiid and two Japanese unionids [Nadamitsu and Kanai. *Bulletin of the Hiroshima Women's University* (1975) 10:1–3; (1978) 1–5.] but different from the 34 diploid number reported for three Australian hybrids (McMichael and Hiscock. 1958. *Australian Journal of Marine and Freshwater Research* 9:372–503).

Analysis of the comparison of arm ratios and percent total complement lengths of 79 measured chromosome spreads from 33 species produced a suggested overall mean karyotype, possible mean karyotypes for six previously-proposed suprageneric groups, and indications of relationships among the groups based solely on the chromosomal measurement data. While extensions of the results should be considered preliminary because of the small number of measured spreads for some groups, these data indicate that North American naiad fauna consist of a single evolutionary group, quite different from the polyphyletic arrangement proposed by Modell (1942. *Archiv fur Molluskenkunde* 74:161–191). The chromosomal relationships are most similar to the classification proposed by Ortmann (1912. Annals of the Carnegie Museum 8:222–365) and only slightly different from the classification proposed by Davis and Fulier (1981. *Malacologia* 20:217–253).

ONTOGENY OF THE LARVAL FOOT OF *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE). Louise Russert Kraemer, Department of Zoology, University of Arkansas, Fayetteville.

Dissemination of *Corbicula fluminea* (Müller), the Asian Clam, has been so rapid through the river systems of the U.S. in the past two decades that malacologists must confront the question, how? In this regard, locomotion of the larval stages and the free-living juveniles merits focused study. In the present investigation, microscopic serial sections, SEM, fresh-tissue dissection and microscopic videotaping were used. It was found that *C. fluminea* develops a characteristic, barrel-shaped trochophore larva, replete with apical tuft, which is retained within the marsupial gill. The longitudinal axis of the body rotates 90° as a pediveliger develops from the trochophore, and the foot anlage appears near the region of the apical tuft. Pediveligers typically are retained in the marsupial gills, where they develop into juveniles about 200 micrometers long. The juveniles exhibit clearly differentiated statocysts and a conspicuous sock-shaped foot that is very active in the substratum or in the water column. Sinuses of the juvenile foot are not well developed, and there is no "Hakenform," "Grabstritt," or "Schwellform" behavior, such as one sees in the adult clam. In contrast, the foot engages in vigorous, rapid maneuvers, comprised of extension, "hunching" (of the animal forward onto its extended foot), extension, etc. Alternatively, the comparatively large juvenile foot is quickly withdrawn completely within the shell valves. SEM examination of the foot revealed that it has a peculiar structure, comprised of a longitudinal series of membranous rings about 2 μm wide, which are joined to each other by loose connective tissue. It is quite evidently the "segmenting" rings of tissue that allow the rapid extension and telescoping withdrawal of the juvenile foot. This study indicates that there is structural basis for the distinctive form of pedal locomotion in the juvenile *C. fluminea,* a basis vastly different from that of the adult clam.

INDUCTION OF COLOR FORMS IN *CORBICULA.* Robert S. Prezant and **Kashane Chalermwat,** University of Southern Mississippi, Hattiesburg.

"White" forms of *Corbicula fluminea,* from Tallahala Creek, Mississippi, were maintained in the laboratory under four different environmental regimes. Specimens were kept for three months in aquaria at either 23°C or 31°C with or without the introduction of a mixed agal/protozoan supplement. Clams maintained at 31°C with a high organic content in surrounding waters produced internal shells with a pure white coloration. Microstructurally these white internal shells were composed of crossed acicular structure. All other regimes tested produced clams with purple highlighted internal shell colorations and "normal" crossed lamellar structures.

Lethargic, unhealthy or dying clams all showed a glossy white color and acicular microstructure. Empty valves collected from creek banks also show a crossed acicular microstructure but are dull white in internal coloration. Active, healthy clams maintain a purple highlighted internal shell color and typical corbiculacean internal shell microstructure. These results are of importance since recent reports of a purple and white morph are thought to have taxonomic value. It is unlikely that color or other morphometric features will prove to be of any systematic value in the determination of North American species of *Corbicula.* Many of the reported morphometric distinctions between or among populations of *Corbicula* in North America may be reflections of microhabitats.

DOES AMBIENT OXYGEN TENSION LIMIT THE DISTRIBUTIONS OF FRESHWATER SNAILS? Robert W. Hanley, The University of Alabama, Tuscaloosa.

This study examines the relationship between ambient oxygen tension (P_{O_2}) and metabolic rate (V_{O_2}) in freshwater snails, in order to determine whether some species are unable to exploit various habitats due to their metabolic response to declining oxygen tension. Laboratory and field data have been collected on eleven species of freshwater snails, from both lotic and lentic habitats with differing oxygen availabilities. Metabolic rates were determined using a closed respirometer technique, in which oxygen consumption by the snails induced a progressive hypoxia.

At 15°C four of the species tested were found to have metabolic rates dependent on P_{O_2} (metabolic oxygen conformers); the other seven species had metabolic rates that were independent of P_{O_2} (metabolic oxygen regulators). At 25°C all of the species tested were metabolic oxygen regulators. Habitat was not correlated with the abilities to regulate V_{O_2}, a finding that is contrary to earlier investigations. The ability to regulate appeared to be morphologically based, with prosobranch species able to regulate V_{O_2} over a wider range of oxygen tensions and more perfectly than pulmonate species. Among the pulmonate species, the planorbids, which have hemoglobin in their blood, are better metabolic oxygen regulators than pulmonates that lack hemoglobin. This study demonstrates that freshwater snails in general are able to tolerate low ambient oxygen tensions, and therefore it is concluded that habitat selection in this group is not determined by oxygen availability.

ECOLOGY AND ZOOGEOGRAPHY OF SOME MAINLAND CHINESE *TRICULA* (GASTROPODA: PROSOBRANCHIA: POMATIOPSIDAE) TRANSMITTING SCHISTOSOMES. K. Elaine Hoagland,[1] Yuanhua Kuo,[2] George M. Davis,[3] Pulin Chen,[2] Hongmu Yang,[4] and **Deji Chen,[5]** [1]Academy of Natural Sciences of Philadelphia, and Lehigh University, Bethlehem, Pennsylvania; [2]Institute of Parasitic Diseases, Chinese Academy of Medical Sciences, Shanghai, P.R. China; [3]Academy of Natural Sciences of Philadelphia; [4]Yunnan Provincial Anti-Epidemic Station, Kunming, P.R. China; [5]Dali Anti-Schistosomiasis Institute, Xiaguan, Yunnan Province, P.R. China.

There are numerous species of *Tricula* and closely-related genera in Southern China and Southeast Asia. Based on previous work, we believed that both the number of taxa in Yunnan Province and the potential for these taxa to transmit mammalian schistosomes were underestimated. This was the case. We found eight species of *Tricula* (delineated anatomically) in the areas of Dali, Kunming, and Jinghong. Although never sympatric congeners, species of *Tricula* lived with closely-related genera at three localities.

One large (7–8 mm) species of *Tricula* lived on stones in a creek and in a culvert draining into Dianchi Lake, with a few specimens in the lake itself. This species differed from other *Tricula* in being able to withstand polluted water with high silt burden. It carried no schistosomes. The other species of *Tricula*, all ~ 3 mm long, lived in mountain springs or tiny creeks and pools below springs. They were found in gently-flowing, clean, cool water. Some individuals were amphibious, but most were in flowing water, if only a hillside seepage. The snails were on undersides of leaves and stones, and on the mud itself. Associated fauna often included *Gyraulus, Radix, Sphaerium,* insect larvae, flatworms, and leeches.

Tricula was never in stagnant water or streams larger than ½ meter wide. Habitats were highly localized, small, and isolated yet permanent, perhaps accounting for high speciation in the geographically-widespread genus.

Forked-tail mammalian-type schistosomes infected three species of *Tricula.* Many of the snail habitats, in canyons where there was natural vegetation, suggest that rats could be the final host. Humans may come into contact when obtaining water for domestic use. Chinese *Tricula* is ecologically similar to *Tricula* in Burma, India, and to a related genus in Malaysia that transmits human schistosomes. If the Chinese snails transmit human schistosomes, transmission patterns differ from those of *Oncomelania hupensis,* the amphibious snail transmitting *Schistosoma japonicum* that is associated with irrigation ditches in much of Southern Asia.

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THE LIMPET GENUS *BRONDELIA* AMONG THE FRESHWATER GASTROPODS. J. B. Burch, Smithsonian Institution, Washington, D.C.

Bourguignat (1853 [1854] *Proceedings of the Zoological Society of London,* (21): 92) described a curious limpet-like gastropod, *Ancylus drouetianus,* from the Cuming collection. The shells lacked any indication of a locality, but Bourguignat believed them to be from North America. The shells were peculiar in that they were decorated with a number of radiating reddish stripes, and because of the apex: "mamillato, minutissimo, coarctato, *adpresso, recurvo (culmine 1, 2 spiraliter laterali),* mediano, postico" [italics mine] (Bourguignat, 1862, *Revue et Magasin de Zoologie,* ser. 2, 14: 20). Bourguignat received additional specimens from Algeria and, in the latter publication, named a new genus for the snail, *Brondelia,* clearly differentiating it from *Ancylus.* In the same paper, Bourguignat named a second species, *Brondelia gibbosa.* This species also "a été recueillie sur des rochers humides, dans l'intérieur de la forêt de l'Édough, prés de Bone, en Algérie."

In June 1973, I traveled to Algeria with two assistants to collect in the Édough Forest near Bône (Annaba). The forest was not overly disturbed by human activities, the snail habitats were good, and various snail species were collected with little difficulty. We were able to collect widely in the area. But, after several full days of searching, no gastropods resembling *Brondelia* were found (see Brown, 1980, *Freshwater Snails of Africa and Their Medical Importance,* Taylor & Francis, London, p. 143).

Because of the failure to find *Brondelia* at the only specific locality ascribed to either of its two species, I became suspicious about the identity of this supposed ancylid. On inspecting Bourguignat's specimens a short time later from the Muséum d'Histoire naturelle, Geneva, it was obvious that *Brondelia drouetiana* was a species of the siphonariid genus *Williamia* Monterosato. On comparing Bourguignat's specimens with specimens of *Williamia* in the Muséum National d'Histoire naturelle, Paris, it was clear that *Brondelia drouetiana* was identical to *Williamia gussonii* (Costa).

Since *Williamia* Monterosato 1884 (type species: *An-*

cylus gussonii Costa 1829) is predated by *Brondelia* Bourguignat 1862, *Brondelia* will replace the generic name *Williamia* in the Siphonariidae.

CHARACTERS AND CLASSIFICATION—A PRELIMINARY REVIEW OF THE GENERA IN THE SUBFAMILY OCTOPODINAE. **Ronald B. Toll,** Department of Biology, University of the South, Sewanee, Tennessee.

The subfamily Octopodinae includes the shallow water, common octopuses. The group has gone without a comprehensive systematic revision since Robson's monumental study published in 1929. Uncertainties concerning the validity of many of the genera have resulted in the common, largely uncritical usage of about twelve generic names within the body of octopodine literature. This classification shows strongly skewed levels of monotypicity with *Octopus* comprising well over 100 species and all other genera having five or less nominal species. At least five genera are monotypic.

Preliminary results of a study on the morphologic variability of selected octopodine characters suggest that a substantial number of the genera are invalidly described. The principal problem associated with the present generic classification is the typological concept originally employed to erect many of these taxa. It is now seen that a number of character states used to establish and delineate genera actually represent points along character continua that extend across several genera or the subfamily as a whole.

A review of the genera of octopodines, now underway, should result in a reduction of the number of valid taxa and decreased levels of monotypic skewedness.

SYSTEMATICS OF *GONATUS TINRO* FROM THE SOUTHEASTERN BERING SEA. **C. G. Bublitz** and **T. Nishiyama,** Institute of Marine Science, University of Alaska, Fairbanks.

Seven species of oegopsid cephalopods were identified from an examination of 2,244 immature specimens from the southeastern Bering Sea. The species identified included: *Gonatus onyx, G. berryi, G. madokai, G. middendorffi, G. tinro, Berryteuthis magister* and *B. anonychus.* Of these species, the literature lacks information on the specific characteristics of immature *G. tinro*. Juveniles of *G. tinro* are commonly identified as *B. magister.*

The specific characteristics of immature *G. tinro* were determined from an examination of 181 specimens ranging in size from 6.7 to 68.3 mm PL. The results show that immature *G. tinro* can be separated from other members of the genus on the basis of arm and tentacle armature development. Juvenile *G. tinro* have 5–6 transverse rows of suckers on the oral surface of the tentacular stalk and arm hook development commencing at about 18 mm PL. Club armature maturation starts around 16 mm PL and is completed by 30–35 mm PL. *Gonatus berryi* develops mature club and arm armature at 7–9 mm PL. *Gonatus middendorffi* has four regimented rows of suckers on the proximal portion of the manus followed by four staggered rows on the oral surface of the stalk.

Separation of *G. onyx* and *G. tinro* in the size range less than 10 mm PL is difficult to make on the basis of sucker counts or morphometrics. Both species from this study had five to six rows of juvenile tentacular stalk suckers with the total number of suckers showing considerable overlap. When enhanced by staining the developing hook bud of *G. onyx* can be distinguished at 8–11 mm PL and is the most reliable method of separation.

Juvenile *Gonatus tinro* and *Berryteuthis* spp. were separated by scanning electron microscopic examination of radulae. The results show that specimens with five to six transverse rows of suckers on the tentacular stalk and arm hook development starting at about 18 mm PL were *G. tinro.* Those specimens with four scattered transverse rows of stalk suckers and no arm hook development evident were *Berryteuthis* spp.

CATALOG OF WORLDWIDE CEPHALOPOD RESOURCES: A PREVIEW. **Clyde F. E. Roper** and **Michael J. Sweeney,** National Museum of Natural History, Smithsonian Institution, Washington, D.C.

An annotated and illustrated catalog of the cephalopod species of interest to fisheries around the world has been prepared for publication by the Food and Agriculture Organization of the United Nations (FAO). It includes information on scientific and vernacular nomenclature, synonymy, specific characters, geographic distribution, habitat and biology, and current or potential use as a fishery resource for 172 species (47 sepioids, 89 teuthoids, 34 octopodids, 2 nautiloids). The catalog is available from: Fishery Resources and Environment Division, FAO Fisheries Department, Viale delle Terme di Caracalla, 00100 Rome, Italy.

DISTRIBUTION AND ABUNDANCE OF SQUIDS CAUGHT IN SURFACE GILLNETS IN THE SUBARCTIC PACIFIC, 1977–1981. **Tsunemi Kubodera,** Nakano-Ku, Tokyo, Japan.

A total of 21,550 squids was obtained from 1,286 gillnets set by Japanese salmon research vessels in the northwestern North Pacific during May to August 1977–1981 and in the Gulf of Alaska in July 1980–1981. Eight species and one genus were identified. *Ommastrephes bartrami, Onychoteuthis borealijaponica* and *Gonatopsis borealis* were the most common species, comprising 46%, 33% and 20% of the catch, respectively.

Seasonal changes of distribution and abundance of the three common species in the surface waters of this region were closely correlated with the heating of surface waters and the development of vertical thermal gradients during summer.

G. borealis is distributed broadly in the Subarctic Region from spring to summer; the southern boundary of occurrence shifts to the north by about 4°–5° of latitude during summer. Apparently this species does not form massive schools or large concentrations. *G. borealis* has two geographically segregated subpopulations, each with a distinct size composition and independent development of reproductive organs. Both groups are maturing during summer.

O. borealijaponica is a Transitional-Subtropical species that migrates into the Subarctic Region during the summer and reaches water just south of the Kuril Islands in August. As a result of this northward migration, catches in surface waters of Subarctic Pacific increase substantially, especially north of the Subarctic boundary where a strong vertical thermal gradient develops between warm surface waters and deeper, cold Subarctic waters. Summer migrants into Subarctic waters are maturing sexually.

O. bartrami is a Subtropical species that migrates northward to the Subarctic boundary in summer. Only large, immature females (larger than about 35 cm DML in July) migrate into Transitional Domain after warming of these waters. This is the most abundant species of squid in the surface gillnet catches around the Subarctic Boundary and Transitional Domain during the summer.

DYNAMICS OF SHALLOW-WATER POPULATIONS OF *OCTOPUS DOFLEINI*. R. F. Ambrose, Simon Fraser University, Burnaby, British Columbia, Canada.

A long-term study of populations of *Octopus dofleini* off the west coast of Vancouver Island, British Columbia, has been conducted by Dr. E. B. Hartwick and various collaborators. All octopuses at two study sites were captured and individually tagged. Abundances at the two sites fluctuated considerably over a five-year period. Peak abundances usually occurred in summer, and in winter in some years, but there was considerable year-to-year variation. In spite of the close proximity of the two sites, the abundance patterns were not identical. A wide size range of octopuses was captured every month. The weights of recaptured octopuses did not differ by sex or season. Among newly-captured octopuses, males weighed on average more than females, and average male weight changed seasonally, declining from 12 kg in winter to 5 kg in the following fall. Immigration into the two sites was variable, but often high. Most octopuses stayed at the study sites for at least one month. Many octopuses returned to a site after an absence of >1 month. These long absences were initiated more frequently and for longer periods of time between July and December; smaller octopuses were gone for longer periods of time. Emigration from the sites occurred throughout the year, with no strong seasonal trends. Recruitment, based on the abundance of small octopuses, occurred all year long. Females predominated among scuba-captured octopuses throughout the 5-year period. However, males were more common among octopuses caught in nearby traps; these different sex ratios are apparently due to behavioral differences between the sexes.

The population dynamics of *O. dofleini* were compared to those of *O. bimaculatus* in southern California. The abundance patterns were similar, but for fundamentally different reasons: declines in the abundance of *O. bimaculatus* were due to the nearly-synchronous deaths of post-reproductive individuals, while in *O. dofleini* it was due to emigration. Recruitment patterns were very similar, probably because newly-hatched young of both species are planktonic.

FJORD/ISLAND ECOLOGY OF A POPULATION OF SEPIOLID SQUID. William C. Summers, Huxley College, Western Washington University, Bellingham.

Circulation in the deep basin of a Swedish fjord is related to the population parameters of the nekto-benthic squid, *Sepietta oweniana.*

COMPENSATORY BUOYANCY CHANGE IN *NAUTILUS MACROMPHALUS*. Peter Ward, Department of Geology, University of California, Davis.

Apertual shell breakage stimulates chamber refilling, hence compensatory buoyancy change in *Nautilus macromphalus.* Observation on 20 aquarium maintained specimens showed the greatest in-water weight change (0.15 g/hr) to occur in the first ten hr after shell breakage. Subsequent buoyancy change was much lower (0.05 g/hr).

THE ROLE OF MANTLE ELASTICITY IN SQUID SWIMMING. M. Edwin Demont and **J. M. Gosline,** Zoology Department, University of British Columbia, Vancouver.

An elaborate network of collagen fibers in the mantle stores energy from the contraction of the circular muscles. This stored energy is available to power mantle re-expansion and presumably improves swimming performance.

STATOLITH DEVELOPMENT AND AGE DETERMINATION IN THE OMMASTREPHID SQUID *ILLEX ILLECEBROSUS* (LESUEUR 1821). C. C. Morris and **F. A. Aldrich,** Memorial University of Newfoundland, St. John's, Canada.

Paper on pages 51–56.

ULTRASTRUCTURAL OBSERVATIONS OF THE CEPHALOPOD LENS. B. A. Houck. University of Portland, Oregon.

Similarities between the octopus eye and the vertebrate eye are extensive. Both visual systems consist of a photoreceptive retina, an iris, lens, cornea, sclera, choroid blood vessels, and an eyelid that can be closed during sleep.

Differences can also be identified, including the type of photoreceptive cells within the retina, the embryonic origin of structures within the eye, the method of accommodation, and the degree of peripheral processing in the retina. However, the similarities are so remarkable that the visual systems of the vertebrates and cephalopods are often used as classical examples of convergent evolution in two distinctly separate lines within the animal kingdom. The similarities are extended by this report of the structure and organization of lens fibers within the ocular lens.

The vertebrate lens is a transparent crystalline structure; the transparency is due primarily to the shape, arrangement, internal structure and biochemistry of the elongated lens fibers. The hexagonal cross-sections of the vertebrate lens fibers are approximately 7 microns wide and 4.5 microns thick in man, with some variation reported in other species.

Like the vertebrate lens, the octopus lens demonstrates a regular array of hexagonal cross-sections of elongated lens fibers in ultrastructural observations. Embryonic octopus lens were fixed in 2.5% glutaraldehyde, washed with sea water buffer with trace collidine, then post-fixed in 1% OsO_4 in the same buffer. Samples were embedded in Epon and sectioned at a later date. TEM examination of the Hawaiian crescent octopus at 36 days development showed hexagonal lens fibers of approximately 0.5 microns by 0.3 microns dimensions.

Although the lens fibers of the cephalopod eye are smaller than those in the vertebrate eye, the stacked array of hexagonal fibers makes the cephalopod lens a true crystalline lens. As in the vertebrate lens, this regular packing in the octopus lens may allow maximum strength in cell to cell contact and also may contribute to the transparency of the lens.

DO THE IRIDOPHORES OF THE SQUID MANTLE REFLECT LIGHT OR DIFFRACT LIGHT IN THE PRODUCTION OF STRUCTURAL COLORS? Roger T. Hanlon, Kay M. Cooper, The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston and **Richard A. Cloney,** The Department of Zoology, The University of Washington, Seattle.

The dermis of squids contains complex cells called iridophores that lie beneath the chromatophore organs. It is well known that these cells produce structural colors upon interaction with light. The ultrastructure of iridophores has been described by several investigators, but it is not yet certain whether cells in the mantle of squids function as thin-film interference devices or as diffraction gratings. In the mantle of *Lolliguncula brevis* there are iridophores of several sizes and shapes. They all contain many ribbon-like iridosomal platelets and these are arranged within the cytoplasm into small parallel groups called iridosomes. The iridosomal platelets in most cells are generally oriented on edge and are therefore perpendicular to the surface of the epidermis. In other cells nearby, the platelets may be oblique or parallel to the surface. The orientation and organization of the platelets suggest that many cells may act as diffraction gratings because the light would usually strike the edges of the platelets. We have done preliminary experiments in which a beam of light was directed towards the iridophores in the dorsal mantle collar at an angle of 20° measured from the horizontal plane of the mantle. A camera was then used to record the resulting structural colors at progressively larger angles of observation. Observed colors were: red at 40°, red at 60°, orange-yellow at 80°, blue-green at 105°, blue at 120°. This progression from longer to shorter wavelengths is the exact order expected from half of the first order of diffracted light from a grating. In contrast, thin-film devices do not produce a spectrum of colors with a given angle of incident light, although the wavelength of reflection shortens with decreasing angle of incidence. We have planned several additional experiments to test the hypothesis that some iridophores behave as diffraction gratings.

CUTTLEBONE MORPHOLOGY AND BATHYMETRY IN *SEPIA*. Peter Ward, Department of Geology, University of California, Davis.

Recent experiments show that the cuttlebone of *S. officinalis* and *S. orbignyana* implode due to excess pressure at quite different depths. An analysis of cuttlebone morphology in approximately half of the known cuttlebone species indicates that cuttlebone morphological differences can be explained mainly as adaptations for different preferred habitat depths.

CARBOHYDRATE CONSERVATION IN A CEPHALOPOD, *OCTOPUS DOFLEINI*. A. W. Martin and **I. Deyrup-Olsen,** University of Washington, Seattle.

When carbohydrates were given to octopuses intravenously, a long time was required for the urine concentration to reach the blood level (Harrison and Martin, 1965. *Journal of Experimental Biology* 42:71–98). This was attributed simply to a slow rate of regulatory processes, but further investigation reveals at least two mechanisms of probable physiological significance.

Measurements of the distribution of isotope labelled dextrans and inulin through the body organs confirms earlier measurement of the blood (5.8% of body weight) and extracellular fluid (28% of body weight) volumes, but shows that some tissues accumulate both dextrans (up to 79% of blood level) and inulin (up to 130% of blood level) at levels considerably in excess of the average body organ concentration. The mechanism is considered to be a lectin-based activity by the branchial hearts, kidneys and gills, in that decreasing order. The mechanism is probably a generalized defensive one as Kowalevsky (1894. *St. Petersburg Academy of Sciences Bulletin* 36:273–295) showed a concentration of pathogenic bacilli by octopus branchial hearts, and Bayne (1973. *Malacological Review* 6:13–17) has shown a concentration of non-pathogenic bacteria in octopus gills.

The second mechanism, active uptake of glucose, was shown by using isotope labelled 2-deoxyglucose. In this case the branchial heart tissue took up glucose much more rapidly than any other tissue, thus reducing the amount of glucose that could reach the urinary filter, the branchial heart appendages. The kidneys and gills also showed greater activity in this respect than other organs. At these sites of possible loss of glucose from the body the mechanisms of glucose accumulation have been carried much farther than in the average tissue.

ESCAPE BEHAVIOR OF *ROSSIA PACIFICA* BERRY, 1911. Ronald Shimek, Bamfield Marine Station, British Columbia, Canada.

Rossia pacifica exhibits a stereotyped flight response consisting of four major behavioral cycles. A) Take-off, consisting of unburying from the sediment; accomplished by use of lateral fins and arms. B) An ink-jet repetitive cycle consisting of: 1. Inking, 2. Blanching to a light color, 3. Repetitive, periodic, jetting, and 4. Gradual darkening. C) Drifting, consisting of maintaining a characteristic posture with arms spread and skin dark, and D) burying, initiated in response to contact with sediment by the lower arms, and consisting of: excavating a hole with the siphon and covering of the animal with sediment thrown on its back with its arms, and simultaneously, blanching to a light color. It is postulated that this response evolved to facilitate escape from fish predators such as *Squalus.*

VISUAL DISCRIMINATION TRAINING OF LABORATORY REARED OCTOPUSES. Roger T. Hanlon and **John W. Forsythe,** The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston, and **J. B. Messenger,** Department of Zoology, University of Sheffield, England.

For 30 years, wild-caught *Octopus vulgaris* have been used in Europe as models in comparative psychology, particularly in visual and tactile discrimination learning. Training results were often variable, which some researchers attributed to the different experience of octopuses in the wild previous to capture. We present here the first demonstration of visual discrimination learning on laboratory-reared octopuses that all had identical experience prior to training. Octopuses were trained consecutively to discriminate between plastic shapes of the same area but differing either in brightness (black rectangle vs. white), form (white cross vs. diamond), or orientation (white rectangle held horizontally vs. vertically). Four *Octopus maya* were trained at 5 months posthatching (150 g each). The results for 12 consecutive sessions (8 trials per session) were: brightness 66%, 93%, 83%, 100% correct attacks; form 52%, 80%, 92%, 83% correct attacks; orientation 50%, 77%, 71%, 73% correct attacks. Eight *O. maya* from the same culture brood were trained similarly at 9 months posthatching (1,200 g each). The results were: brightness 54%, 59% 75%, 69%; and form 50%, 80%, 76%, 81% correct attacks. In general, these preliminary observations suggest that the younger, smaller octopuses showed keener discrimination. Five *Octopus bimaculoides* were trained 7 months posthatching (60 g each). The results in consecutive sessions were: brightness 48%, 56%, 79%, 81%, 83% correct attacks; form 55%, 62%, 67%, 69%; orientation 54%, 53%, 62%, 53%. This species generally did as well as young *O. maya* on brightness discrimination, but form discrimination was poor, and no orientation discrimination was evident, although training by a different method may yield different results. Overall, the results are encouraging because they indicate that different species of laboratory-reared octopuses are suitable for visual discrimination training. Furthermore, octopuses may be trained throughout the life cycle to study ontogenetic changes in learning ability.

OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF *OCTOPUS BURRYI,* VOSS 1950. John W. Forsythe, The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston.

Information on the reproductive biology of *Octopus burryi* was obtained by laboratory rearing a wild-caught mature female octopus. The female was trawl-caught in February 1981 from a depth of 47 m in the northern Gulf of Mexico approximately 80 miles south of Galveston, Texas. The animal was reared in a 150 ℓ closed seawater system using artificial seawater. At the time of capture the octopus had a live wet weight of 204 g and a dorsal mantle length of 107 mm making it the largest specimen of this species on record. Twenty-two days after capture, the female began laying a large brood of eggs which she carried in her arms throughout their developmental period. Approximately 35,000 eggs were laid weighing a total of 91.3 g, 44% of the female's prespawning weight. Egg length excluding the stalk was 2.2–2.5 mm. Hatching occurred from 24 to 36 days after egg-laying indicating a development time of approximately four weeks at 23°C. Hatchlings were very small, having a mean dorsal mantle length of 1.5 mm and mean total length of 2.5 mm. The female occasionally accepted food up to 20 days post egg-laying, but refused it thereafter and died 19 days after the last hatchlings were observed (WW = 115 g, ML = 70 mm). An attempt was made to culture the planktonic hatchlings in a circular dish-bottomed tray (1 m diameter) suspended in a 2000 ℓ closed seawater system. The octopuses were fed live plankton, principally copepods, which they actively attacked and captured. Maximum survival was 18 days with no significant growth observed.

NOTES ON THE LABORATORY CULTURE OF *OCTOPUS BIMACULOIDES*, THE CALIFORNIA MUD-FLAT OCTOPUS. John W. Forsythe, Randal H. DeRusha and **Roger T. Hanlon,** The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston.

More than 50 *Octopus bimaculoides* were reared from hatching to sexual maturity and a subsequent F_2 generation in closed recirculating seawater systems. The culture systems held 2500 ℓ of artificial seawater. The main population of octopuses was reared at 17 to 18°C, but a second group of animals was reared at 22 to 24°C. The primary foods were small, live mysidacean shrimps for octopus hatchlings and progressively larger, live palaeomonid and penaeid shrimps for growing octopuses. *Octopus bimaculoides* also accepted a wide range of supplemental food organisms including amphipods, crabs, bivalve and gastropod molluscs, polychaete worms and fishes. Survival through the life cycle was good. Greatest mortality occurred during the first two weeks, mainly from premature hatching and cannibalism. Over 50% of the octopuses alive after one month survived to one year of age. The life span appears to be at least 12 months; at this writing over 30 octopuses have lived beyond 13 months. The first sign of sexual maturation in males was the appearance of the hectocotylus at four to five months posthatching. Among the warm-water reared octopuses, mating was first observed at 8 months and egg-laying at 10 months; in the cold-water population it was 10 and 12.5 months, respectively. Growth was exponential during the first four months. The warm-water group grew at an overall rate of

4.5% body weight/day during this time, compared to 3.5%/day for the cold-water group; they were almost three times larger at the end of this phase. Beyond four months, growth slowed and became logarithmic in form, with growth rates near 1.0%/day. Males were consistently larger than females. In summary, this species appears very well suited for laboratory culture. It tolerates high density rearing conditions without aggression or disease problems, it eats a wide range of live and dead foods, and it grows well over a wide temperature range.

LABORATORY CULTURE OF THE CALIFORNIA MARKET SQUID *LOLIGO OPALESCENS* THROUGH THE ENTIRE LIFE CYCLE. Raymond F. Hixon, Won Tack Yang, Philip E. Turk, Mark J. Krejci, A. Michelle Parsons, Lea A. Bradford and **Roger T. Hanlon,** The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston.

Loligo opalescens, Berry was cultured through the entire life cycle in two separate experiments (1981 and 1982). Hatchling squids were reared for two months in a circular 1,300 ℓ closed-system tank, then transferred and cultured to sexually mature adults in 10,000 ℓ and 13,000 ℓ closed-system raceways of different design. At six months of age, adult squids mated and females began to lay egg capsules. The eggs developed into normal second-generation hatchlings in both experiments. Water temperature was between 14 and 19°C; salinity varied from 34 to 36‰; pH fluctuated from 7.8 to 8.2; and levels of ammonia-, nitrite-, and nitrate-nitrogen were usually below 0.1, 0.1 and 20.0 mg/ℓ, respectively. Survival after six months was 6.8% of 2,061 hatchlings in 1981 and 2.6% of 1,704 in 1982. Maximal life span was eight months. Mean mantle length (ML) and wet weight (WW) of adults from the two experiments were 87 mm ML ($S\bar{x} = 2.7$) and 23.8 g WW ($S\bar{x} = 1.9$) for males ($n = 35$), and 83 mm ML ($S\bar{x} = 1.9$) and 21.2 g WW ($S\bar{x} = 1.5$) for females ($n = 58$). Maximum size for males was 115 mm ML and 58.2 g WW, and 116 mm ML and 63.0 g WW for females. Mantle length increased slowly at a rate of 2.0 (1981) and 5.7 mm/mo (1982) during the first two months posthatching; thereafter, mantle length increased at a nearly constant rate of 12.6 (1981) and 13.8 mm/mo (1982). The length-weight relationship of laboratory cultured squids was similar to that observed in the wild population. Squid diet consisted of live crustaceans (zooplankton or mysid, penaeid, and palaemonid shrimps) and fishes (several species, from six different families). The feeding rate of subadult and adult squids averaged 14.9% wet body weight per day. The major causes of mortality were starvation, fin damage, cannibalism and mortality associated with spawning.

GROWTH RINGS IN THE STATOLITHS OF YOUNG LABORATORY CULTURED SQUIDS (*LOLIGO OPALESCENS*). Raymond F. Hixon and **Margarita R. Villoch,** The Marine Biomedical Institute, The University of Texas Medical Branch, Galveston.

Statoliths were obtained from California market squids that were cultured from hatchlings to adults, for a maximum of 235 days. The age of cultured squids was known to within 5 days. Total statolith length (TSL, measured across the anterior surface of the statolith from the edge of the dorsal dome to the tip of the rostrum) increased from approximately 150 μm at hatching (2.5–3.2 mm mantle length, ML) to nearly 1,200 μm at day 235 (age 235–240 days; male, 100 mm ML). Forty-nine statoliths were collected from 29 squids between days 21 (age 21–26) and 65 (age 65–70). Growth rings were visible in a single optical plane in only two of the 49 statoliths when examined whole under a compound microscope (Leitz Orthoplan with filters NG36 and S546). All statoliths were then decalcified in a 1:1 mixture of 4% EDTA in distilled water and 0.2 M sodium cacodylate buffer (pH 7.4). Rings in the decalcified statoliths were more visible, prominent and easier to separate and count than rings observed before treatment. This method was not effective with statoliths from squids older than 65 days (TSL > 600 μm) because decalcified statoliths became amorphous, and rings were no longer clear. For the period between 21 and 65 days, the number of rings in 43 decalcified statoliths (six not legible) were counted from photographic prints taken with a Leitz Combiphot II and Kodak copy film No. 4125. The linear relationship between the number of rings (R) and the age in days (D) was: $R = -7.24 + 1.13\,D$, with an r^2 value of 0.90. Counts of rings differed from the actual age by an average of ± 4.2 (range -12 to $+8$). These preliminary counts indicate that rings in statoliths of young laboratory cultured squids were formed daily. One possible implication is that feeding (12 hours food, 12 hours no food) was responsible for ring formation because there was no diurnal fluctuation in light or temperature.

FATAL PENETRATING SKIN ULCERS IN LABORATORY REARED OCTOPUSES. Roger T. Hanlon,[1] John W. Forsythe,[2] Kay M. Cooper,[1] Anthony R. DiNuzzo,[2] Dean S. Folse,[2] and **Michael T. Kelly,[2]** The Marine Biomedical Institute,[1] The Department of Pathology,[2] The University of Texas Medical Branch, Galveston.

Young *Octopus joubini* and *Octopus briareus* (35 to 60 days old) developed skin ulcers when reared in high density groups. Octopuses reared in individual containers in the same culture system were disease-free. The ulcers first affected the epidermis of the mantle then penetrated downward through the dermis and underlying muscle tissue. Untreated octopuses usually died within four days. The four gross stages of ulceration were (1) dermal chromatophores stopped functioning and pigment granules dispersed, (2) dermis was destroyed leaving clear areas of skin, (3) necrosis progressed inward causing deep and wide ulcers, (4) ulcers spread to the ventral mantle of *Octopus joubini* or the head and arms of *Octopus briareus.* No viruses or fungi were observed in skin samples, but five species of bacteria were isolated from ulcers: *Vibrio alginolyticus, Vibrio damsela, Pseudomonas stutzeri* and *Aeromonas caviae* from *Octopus joubini; Vibrio parahaemolyticus, Vibrio damsela* and *Pseudomonas stutzeri* from *Octopus briareus.* Bacteria could be seen in all stages of ulceration by light microscopy and by scanning and transmission electron microscopy. Sixty-five healthy *Octopus joubini* were given small incisions and immersed for 60 minutes in various concentrations of bacteria cultured from the ulcers, and *Vibrio alginolyticus* at 10^6 cfu/mℓ produced similar skin ulcers within two days. Penicillin, chloramphenicol, minocycline hydrochloride, and 10% nifurpirinol (Furanace®) were evaluated as treatment. Nifurpirinol was effective; of 28 *Octopus joubini* dipped each day for 10 minutes in 10 mg/ℓ nifurpirinol over an 82-day period, only 18% died, and 73% of the remainder showed nearly complete healing. Nifurpirinol was effective on *Octopus briareus* as well. This higher concentration healed the ulcers but killed 78% of the octopuses; lower doses should be used in the future. There was an apparent species-specific susceptibility to the disease because *Octopus maya* and *Octopus bimaculoides* in the same culture systems were disease-free. The suspected cause of ulceration was increased contact among crowded octopuses that resulted in skin abrasions which were invaded by opportunistic bacteria.

LARVAL DEVELOPMENT OF THE "GUTLESS" PROTOBRANCH BIVALVE *SOLEMYA REIDI* BERNARD 1980 (BIVALVIA: PROTOBRANCHIA). Richard Gustafson, Department of Biology, University of Victoria, British Columbia.

Development and morphogenesis of *Solemya reidi* was followed throughout the six-day lecithotrophic larval stage at 10°C using light and scanning electron microscopy. *S. reidi* is not gutless throughout its life.

THE BENTHIC ECOLOGY OF A GUTLESS PROTOBRANCH BIVALVE, *SOLEMYA REIDI.* Penelope A. Gee, Department of Biology, University of Victoria, British Columbia.

Solemya reidi, a recently described benthic protobranch bivalve from the northeastern Pacific Ocean, possesses neither a gut nor internal enzymatic apparatus. High densities of this animal appear limited to sediments below wood-fibre beds. An effort has been made to relate the animal's density and distribution to a number of environmental parameters. Current research incorporates recent information on the animal's possible modes of nutrition.

BROODING IN *TRANSENNELLA TANTILLA* (BIVALVIA: VENERIDAE). Alan R. Kabat, Department of Zoology and The Friday Harbor Laboratories, University of Wasington, Seattle.

The brooding of a small Pacific Coast bivalve, *Transennella tantilla* (Gould, 1852) is analyzed. This clam broods up to 170 embryos between the inner gill and the body wall. Within each brood mass, the embryos are individually encapsulated, and the whole mass shows a graded sequence of developmental stages, from youngest (dorsal/proximal) to oldest (ventral/distal). Most other brooding bivalves show synchrony of embryonic development within a brood mass. Direct development to a non-pelagic juvenile stage occurs and there is no planktonic veliger stage. The hatched juveniles leave the mother through her exhalent siphon.

The allometry of brooding is considered from a theoretical viewpoint and it is shown that reproductive effort (brood number and brood weight) increase in proportion to the square of adult size. It is concluded that the gill surface area acts as a morphological constraint on reproductive output.

The maternal feeding currents, by aerating the embryos, are potentially used for embryo respiration and excretion. In vitro culturing of the embryos was unsuccessful.

Since there is no planktonic larval stage, it is predicted that other agents are involved in the dispersal of juveniles and adults. These agents include external factors (birds, fish, seaweed rafting, storms, currents) and internal factors (byssus thread drifting), and must be responsible for the contemporary species range.

BIVALVE ASSEMBLAGES IN NORTON SOUND, ALASKA: SIZE STRUCTURE AND EFFECTS OF PREDATORS. Allan K. Fukuyama, Moss Landing Marine Laboratories, California.

The bivalves *Mya truncata, Macoma calcarea, Serripes groenlandicus,* and *Yoldia hyperborea* are characteristic animals of subtidal, soft sediments in northwestern Norton Sound, Alaska. Size class domination is exhibited with many small, recently settled animals, very few intermediate sizes, and a distinct adult population. It is believed that predation by seastars, especially *Asterias amurensis,* is responsible for the size classes seen. Gut content examinations of *A. amurensis* showed it to be an important predator on bivalves <10 mm. Once this initial predation is surpassed, refuges from seastars are attained. Laboratory studies and field observations revealed that *Y. hyperborea* and *S. groenlandicus* are able to use behavioral escape responses of burrowing and leaping, respectively, while *M. calcarea* and *M. truncata* use a depth refuge, in conjunction with a related size refuge in order to avoid predation by seastars. Once these bivalves reach about 40 mm, they become subjected to seasonal predation by walruses. *S. groenlandicus* is the preferred prey since it is a shallow burrower and populations of this species have been reduced. Consequently, walruses appear to be concentrating their feeding efforts now on populations of *M. truncata.*

ASPECTS OF THE DEVELOPMENTAL BIOLOGIES OF *OENOPOTA LEVIDENSIS* (CARPENTER, 1864) AND *OENOPOTA FIDICULA* (GOULD, 1849) (GASTROPODA: TURRIDAE). Ronald Shimek, Bamfield Marine Station, British Columbia, Canada.

Oenopota levidensis deposits egg capsules proportional to the size of the female, large females (1 > 20 mm) depositing up to 250 eggs per capsule. There are no nurse eggs. The capsules hatch 21–69 days later releasing veligers that swim actively for about one week. The planktotrophic veligers develop demersally for a further period of up to seven weeks. Total developmental time is from

40 to 108 days and is temperature dependent. Settlement may be synchronous for all larvae in a given geographical region. Metamorphosis takes about three or four days, and the veligers appear to settle preferentially on sediment of silt-clay size range.

Development of *Oenopota fidicula* is similar, although the egg capsules are smaller with fewer eggs. Potentially synchronous settlement was not observed.

NORTH ATLANTIC-PACIFIC NUDIBRANCH COGNATES. Sandra V. Millen, University of British Columbia, Vancouver, Canada.

Several cognate species of nudibranchs living in the Atlantic and Pacific oceans were examined using scanning electron microscopy and conventional dissection to determine morphological differences. The cognates *Onchidoris muricata* (Müller, 1776) of the Atlantic and *O. varians* (Bergh, 1878) of the Pacific appear to be identical when similar sized specimens are compared, but in the Norwegian Sea they are larger with the notal tubercles disproportionately larger. These larger specimens are usually confused with *Adalaria lovéni* (Alder & Hancock, 1862). During this study it was discovered that the description of *Onchidoris hystricina* (Bergh, 1878) fell within the description of *O. muricata* and is therefore a junior synonym. The animal that is commonly considered to be *O. hystricina* upon examination was found to be a *Diaphorodoris.* Another Pacific species, which has been referred to as *Onchidoris* sp., was found to have the multiple lateral teeth of an *Adalaria.* A reassessment of Bergh's 1978 criteria for distinguishing the genera *Onchidoris* and *Adalaria* found that all the criteria except the number of lateral teeth were invalid. This is a tenuous distinction as some *Adalaria* have as few as five laterals per side. If intermediate forms are found in the future it will be necessary to synonymise these genera. The second cognates, *Adalaria proxima* (Alder & Hancock, 1854) from the Atlantic and the Pacific *A. pacifica* Bergh, 1880 were found to vary only slightly from each other. The differences may be due to preservation artifacts. It is concluded that these two species are synonymous.

BIOLOGICAL ADAPTATIONS OF INTERSTITIAL MOLLUSCS. M. Patricia Morse, Marine Science Laboraory, Northeastern University, Nahant, Massachusetts.

Interstitial molluscs are characteristic of shifting coarse sand environments. Major molluscan taxa represented include solenogasters, acochlidiaceans and species of the nudibranch genus, *Pseudovermis.* These organisms are small (1.5–3.0 mm in length), have reduced numbers of cells, a small number of eggs, often spicules rather than an extensive shell and a variety of adhesive organs. They are distributed in intertidal and subtidal sands of tropical, subtropical and temperate environments. Biological and ecological studies of sites including San Juan, Washington, Crow Neck, Maine, Fort Pierce, Florida, Carrie Bow Cay, Belise and Viti Levu, Fiji have led to defining an assemblage of these molluscs that occur in well-oxygenated coarse to medium sands devoid of sulfides. Associated with the assemblage are interstitial hydroids upon which the solenogasters and nudibranchs feed. Reproductive modifications for this environment include production of spermatophores and deposition of small numbers of encapsulated embryos (Acochlidiacea). Spicule formation is common in the Acochlidiacea and characteristic of all the interstitial solenogasters. All of these interstitial molluscs offer examples of regressive evolution toward vermiformity for living in pore spaces of the environment.

SHELL REDUCTION AND LOSS IN FISSURELLIDS: A REVIEW OF GENERA AND SPECIES IN THE *FISSURELLIDEA* GROUP. James H. McLean, Los Angeles County Museum of Natural History, California.

Paper on pages 21–34.

THE EVOLUTION OF BROODING IN ACMAEID LIMPETS. David R. Lindberg, Museum of Paleontology, University of California, Berkeley.

Brooding has evolved in only one acmaeid shell structure group, and the methods of fertilization, embryo nourishment, and brooding differ among the brooding species.

REVISION OF HIGHER TAXA IN GENUS *CERITHIDEA* (MESOGASTROPODA: POTAMIDIDAE) BASED ON COMPARATIVE MORPHOLOGY AND BIOLOGICAL DATA. Richard S. Houbrick, Smithsonian Institution, Washington, D.C.

Paper on pages 1–20.

BIOGEOGRAPHICAL AFFINITIES OF THE OPISTHOBRANCH GASTROPOD FAUNA OF SOUTHERN AFRICA. Terrence M. Gosliner, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco.

The tip of southern Africa provides an important area for the study of the distribution of marine organisms. Not only is it the juncture of the Indian and Atlantic Oceans, but it is a region characterized by abrupt changes in oceanic temperature.

The vast majority of opisthobranch gastropods have planktotrophic veliger larvae that can be dispersed across entire ocean basins. Several factors further influence the distributional patterns of these organisms. Revision of the systematics of taxa can dramatically alter their apparent distributional patterns. For example, synonymy of several taxa with *Aeolidiella indica* produces a single circumtropical species rather than seven endemics. Lack of data with regard to large geographical areas often produces erroneous distributional conclusions. Human interference with distributional patterns may also alter biogeographical inferences. Despite these potential limitations it is possible to determine the distributional patterns of over three hundred species of opisthobranchs from southern Africa with a reasonable degree of confidence.

Traditionally, the Cape of Good Hope has been considered to constitute a major biogeographical barrier between discrete cold and warm water, largely endemic, faunas. However, approximately three-fourths of the opisthobranchs occurring on the Atlantic side of the Cape Peninsula are also found in False Bay, on the Indian Ocean coast. Far more profound faunal differences occur between the largely endemic fauna of the eastern Cape Province and that of the Transkei coast, which consists largely of Indo-West Pacific taxa.

The opisthobranch fauna of southern Africa is composed of a unique blend of tropical, temperate and Antarctic taxa, which appears to be a result of both vicariant events and recent dispersal.

BURROWING ACTIVITIES OF *PERIPLOMA MARGARITACEUM* (LAMARCK, 1801) (BIVALVIA: ANOMALODESMATA: PERIPLOMATIDAE). **Joseph Rosewater,** Smithsonian Institution, Washington, D.C.

Paper on pages 35–40.

A REVIEW OF THE BIVALVE GENERA *AXINULUS* VERRILL & BUSH, 1898, *LEPTAXINUS* VERRILL & BUSH, 1898 AND *ADONTORHINA* BERRY, 1947 WITH NOTES ON A NEW SPECIES OF THYASIRIDAE. **Paul H. Scott,** Santa Barbara Museum of Natural History, California.

A new species of Thyasiridae has been found in deep water in the northeast Pacific. Generic placement of the species proved difficult as it exhibited characters of the genera *Axinulus*, *Leptaxinus* and *Adontorhina*. Type material of the three genera was examined to determine the correct generic placement for the new species. Inspection of the hinge plate proved to be the most useful character in differentiating the genera.

Distinctive characters of the genera are defined below.

Axinulus Verrill & Bush, 1898 (8 North American species, 7 species examined)
  Type species *Axinulus brevis* V & B, 1898
    hinge plate thin, smooth and edentulous
      —minute hinge tubercles present in some species
Leptaxinus Verrill & Bush, 1898 (1 North American species)
  Type species *Leptaxinus minutus* V & B, 1898
    hinge plate narrow but well developed
      —right valve with small tubercle beneath umbo which fits into corresponding notch in the left valve hinge.
      —right valve with long lateral grooves along anterior and posterior of the hinge plate into which the shell margin of the left valve is seated.
Adontorhina Berry, 1947 (1 North American species)
  Type species *Adontorhina cyclia* Berry, 1947
    hinge plate broad with a unique granular appearance
      —hinge granules distinct anteriorly, weakly expressed posteriorly

The new northeastern Pacific species has a broad granular hinge plate placing it in the genus *Adontorhina* Berry, 1947.

PREDATION OF MOLLUSCAN SPECIES BY THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*. **George D. Buckley,** Pleasant Bay Field Station, South Orleans, Massachusetts.

The horseshoe crab, *Limulus polyphemus*, has long been regarded to be a major predator on commercial shellfish. Howsoever, biomedical researchers find *Limulus* blood so important that it has a market value of several thousand dollars per processed liter.

As part of a continuing study, the Pleasant Bay Field Station has researched the predator-prey relationship between the horseshoe crabs and molluscan species, at Pleasant Bay, Orleans, Massachusetts.

With the help of Earthwatch Expedition field assistants the following research regime was conducted:

1. Stomach contents were analyzed from 100 *Limulus*.
2. Feeding observations were made in the field on 200 crabs.
3. Predator-prey studies were conducted using young and adult specimens of the polychaete genera *Nereis* and *Glycera*, the glass sea cucumber, *Leptosynapta*, the softshell clam, *Mya*, the quahog, *Mercenaria*, the razor clam, *Ensis*, and the gem clam, *Gemma*.

The results of stomach content analysis showed the horseshoe crab to be a carnivorous scavenger. The crabs fed on *Mya*, *Mercenaria*, and *Ensis* but also on the small bivalves *Solemya velum* amd most often *Gemma gemma*, the latter easily confused with seed quahogs. Also found were the annelid genera *Nereis*, *Arenicola*, *Glycera*, *Scoloplos*, and *Syllis*, and the holothuroid genus *Leptosynapta*. Quantities tended to be in close proportion to their relative abundance in the area from which the *Limulus* were collected. Small algae remnants were also present.

In the field, feeding observation confirmed the stomach content analysis. In predator-prey studies, *Limulus* "found" the worms and mollusks with equal rates of success. The most preferred bait was *Gemma gemma*. In all cases, prey less than 4 cm was preferred to larger individuals. Horseshoe crabs that were burrowed into the substratum were found not to be feeding in 52% of the individuals studied.

It is apparent that *Limulus* are a significantly lesser threat to commercial shellfish than previously believed. Indeed, they are a major part of the natural predator-prey relationships of bay ecology.

GROWTH IN *MERCENARIA MERCENARIA* (L.). **Arnold G. Eversole, Lawrence W. Grimes,** Clemson University, South Carolina and **Peter J. Eldridge,** National Marine Fisheries Service, Charleston, South Carolina.

Growth and survival of the hard-shelled clam, *Mercenaria mercenaria*, was determined for 13-month old individuals grown for 4.5 years in protected trays in a subtidal site of Clark Sound, South Carolina. Calculated annual mortality rate was 4%. No increase in mortality could be attributed to Hurricane David which brushed the South Carolina coastline in September 1979.

Most of the shell growth (change in shell length, SL) occurred in the first 2 years. Growth appeared to be a function of age and size in that younger clams of the same size grew faster than older clams. Similarly, smaller clams grew faster than larger clams of the same age. The fastest growers in the population were consistently smaller than the slowest growers through a size (60 mm SL) and age (53 months) when growth leveled off. However, individual growth rates varied widely so that the fastest growers in one measuring time interval were rarely the fastest growers in another time interval.

Correlation coefficient computed between initial SL (at planting) and final SL was positive (.40) suggesting clams held a similar position in the size distribution after 4.5 years growth. Following the SL of individual clams through 9 measuring intervals disclosed that the larger clams maintained their position in the size distribution more consistently than smaller clams. The negative correlation coefficient (−.44) observed between initial SL and growth indicated that smaller clams were exhibiting compensatory growth or were overtaking the larger clams. However, some of the smaller clams did not exhibit compensatory growth and, therefore, remained as small individuals in the size distribution. Also, not all of the larger clams were overtaken by compensating clams because as these small clams got bigger the difference in growth was reduced to the point where the larger clams which continued to grow maintained their relative position in the size distribution. For these reasons, the gradual decline in variability with age and growth, which has been assumed to occur as a result of compensatory growth, was not observed. Instead, the standard deviations about the mean SL increased slightly over the 4.5 years. The evidence of this study suggested that the overall reduction in variability in size with time is not a prerequisite for growth compensation, and that the mechanism of compensation may be occurring more frequently among molluscs than previously detected or thought.

FAUNAL ASSOCIATION WITH *ATRINA SEMINUDA* (LAMARCK, 1819). **E. C. Rios, B. L. Albuquerque** and **G. P. Oliveira,** Museu Oceanográfico de Rio Grande, Brasil.

The Pinnidae, principally sessile bivalves, serve as hosts to a number of crustaceans that live as commensals in the mantle cavity and others attached to the outside of their valves.

In 1980, the junior authors of this study collected many specimens of *Atrina seminuda* from off Salvador, Bahia State, in 20 meters of water. We removed 18 species of mollusks and other organisms from the valves. These included five species of Gastropoda, 12 Pelecypoda and one Polyplacophoran.

The other organisms found on *Atrina seminuda* included algae, anemones, barnacles, brittle stars, bryozoa, crustaceans, polychaetes and tunicates.

PACIFIC ISLANDS REVISITED—BIOGRAPHY OF A RECENTLY EXTINGUISHED LAND SNAIL FAUNA. **Alan Solem,** Department of Zoology, Field Museum of Natural History, Chicago, Illinois.

Analysis of the land snail families Endodontidae and Charopidae on the Pacific Islands show a pattern of minor geographic changes that do not correlate with tectonic events. Most of this radiation has become extinct within the past 50 to 150 years because of man-made habitat alterations or introductions.

PRELIMINARY STUDIES ON THE KARYOTYPES OF BRADYBAENIDAE (GASTROPODA: PULMONATA). **Noorullah Babrakzai** and **W. B. Miller,** Department of Biology, Central Missouri State University, Warrensburg and Department of General Biology, University of Arizona, Tucson.

Chromosome study of *Bradybaena similaris, B. (Acusta) despecta sieboldiana,* and two species of *Euhadra,* reveals the unique nature of the karyotype of *B. similaris;* in having 26 pairs of telocentric and only two pairs of metacentric chromosomes.

PHYLOGENETIC STUDIES ON *MESODON* AND *TRIODOPSIS* (GASTROPODA: PULMONATA: POLYGYRIDAE): A PROGRESS REPORT. **Kenneth C. Emberton,** University of Chicago, Illinois.

Mesodon and *Triodopsis* may be separated by reproductive anatomy and behavior. *Mesodon* has a smooth penis and elaborate courtship with intertwining of penes and external deposition of sperm masses; *Triodopsis* has a sculptured penis and little to no courtship with insertion of penes and internal deposition of sperm masses. The two genera have radiated into many of the same ecological habitats in the eastern U.S., resulting in very similar numbers of species and patterns of species diversity and endemism, and resulting in multiple conchological diversities (over a wide range of shell shapes), several of which occur in microsympatry.

In an effort to learn the evolutionary relationships among *Mesodon* and *Triodopsis*, I am using electrophoretic characters and secondary sexual characters. Three months were spent in the field in 1982, resulting in 2,000+ lots; 10,000+ specimens; and 2,500+ tissue samples, including most of the nominal species. My 1983 field season appears to have doubled these figures. All live specimens were relaxed and preserved in ethanol. All specimens will be catalogued at the Field Museum of Natural History, Chicago.

Dissections prove that *Triodopsis* penial sculpture is rich in characters for phylogenetic analysis; *Mesodon*'s will be dissected in the same way.

Starch-gel electrophoresis was performed at the Academy of Natural Sciences, Philadelphia. Thirty-five loci were assayed, 16 of which were chosen for the complete analysis of 950+ snails from 150+ populations comprising 37 nominal *Mesodon* species and 34 nominal *Triodopsis* species. Overall, there were two to 20 alleles per locus ($\bar{X} = 8.5$) and heterozygosity was low (ca 5%). A preliminary analysis of eight populations of *Mesodon zaletus,* ranging from n.e. West Virginia to s.w. Missouri, shows ca 1.3 alleles per locus, general conformation to Hardy-Weinberg equilibrium, and a Nei similarity of 0.8 to 1.0 among populations. A complete analysis of electrophoretic data is in progress.

SYSTEMATIC RELATIONSHIPS OF THE *ORTHALICUS* OF FLORIDA.

Jane E. Diesler, Florida State Museum, Gainesville.

The gross anatomy of *Orthalicus floridensis* Pilsbry and *O. reses* (Say) was examined to establish a basis for determining the status of *O. reses nesodryas* Pilsbry. The genital anatomy and shell pigmentation were found to define two species of *Orthalicus* in Florida, *O. floridensis* and *O. reses.* Shell pigmentation and geographic distribution separate *O. reses* s.s. from *O. r. nesodryas. O. r. nesodryas* is therefore maintained as a subspecies.

The results of covariance analysis of quantitative shell traits were compared to the dendrogram produced by cluster analysis of these traits for the Florida taxa and *O. undatus jamaicensis* Pilsbry. Covariance analysis separates these taxa in a manner consistent with soft anatomy. However, the dendrogram indicates that the degree of overlap is such that quantitative shell traits are not sufficiently reliable to separate these species of *Orthalicus.*

HISTOLOGY AND ULTRASTRUCTURE OF THE VAS DEFERENS IN SELECTED TERRESTRIAL PULMONATES.

Richard L. Reeder, Faculty of Natural Sciences, University of Tulsa, Oklahoma.

The vas deferens was examined in two species of Helminthoglyptidae (*Monadenia fidelis* and *Sonorella virilis*) and five species of Polygyridae (*Ashmunella chiricahuana, Mesodon elevatus, M. zaletus, Triodopsis albolabris,* and *T. fosteri*). In *S. virilis* and *A. chiricahuana* the duct is uniform throughout its length. In *S. virilis* the duct is muscular with a tall columnar epithelium lining the lumen. Uniform microvilli can be demonstrated with the TEM. In *A. chiricahuana* the duct is lined with tall, pale, columnar cells and is moderately muscular. In *M. fidelis* the portion of the vas deferens joining the free oviduct is slightly enlarged while in both species of *Triodopsis* and *Mesodon* the duct is abruptly enlarged at the junction. In all of these latter five species, the lumen of the enlarged portion is thrown into large, numerous folds appearing somewhat like villi in cross section. The lumina of the ducts in these animals is lined with a tall columnar epithelium with at least two cell types apparent in *M. fidelis* and *T. fosteri* (*T. albolabris* and the species of *Mesodon* have not been examined for cell type as yet). In *M. fidelis* there are pale goblet-like cells scattered through the columnar epithelial cells. Examination with the TEM indicates microvilli are numerous. In *T. fosteri* some of the cells have microvilli and some have both cilia and microvilli in the enlarged portion of the duct while only microvilli could be demonstrated in the rest of the duct. The epithelium in *M. fidelis, T. fosteri* and *S. virilis* appears to be of the transporting type.

RADIOCENTRUM AVALONENSE IS ALIVE AND WELL ? ON CATALINA ISLAND.

F. G. Hochberg, Barry Roth, Santa Barbara Museum of Natural History, California, and **Walter B. Miller,** Department of General Biology, University of Arizona, Tucson.

In 1902 Henry Hemphill discovered an unusual oreohelicid snail on Santa Catalina Island, California. The specific name, *avalonense,* suggests that the snail was originally collected in the vicinity of the town of Avalon. However, in spite of repeated attempts the snail could not be found again and was reported to be extinct. In 1982 a small population of live snails was located about 2½ miles south and west of Avalon. Extensive surveys have failed to turn up the snail in other areas on the island, hence, we conclude that it is restricted to the southeastern tip of the island. Here it occurs only on steep, sparsely vegetated, south-facing slopes dominated by Black Sage (*Salvia mellifera*) and Prickly Pear Cactus (*Opuntia littoralis*). The small, sluggish snail lives deep in talus piles and emerges only in wet weather to feed on *Salvia.*

Conchologically the species is typical of the family Oreohelicidae. The shell is lens-shaped and distinctly carinate. At maximum size the shell diameter is 14 mm and there are 5½ whorls. The radially ribbed embryonic shell is diagnostic of the genus *Radiocentrum.* However, until live specimens were discovered generic placement could not be verified. Specimens from Catalina Island were found to have a reproductive system identical to the oviparous genus *Radiocentrum.* In addition to the large albumen gland, swollen lower third of the spermathecal duct and much enlarged, hachet-shaped upper penis characteristic of the genus, *R. avalonense* is further defined by a distinctly swollen lower penis with three conspicuous longitudinal ridges.

The genus *Radiocentrum* was once widely distributed throughout western North America. Climatic changes have dramatically restricted the range of the genus. The distribution of Quarternary taxa has been further reduced and fragmented by the imprint of the Sonoran and Chihuahuan deserts. The majority of the species in the genus are relicts which persist in small isolated localities. Typical of such relicts only a few scattered, low density colonies of *R. avalonense* have been found on Catalina Island. Several related species in Texas and Mexico are known only from empty shells indicating the continued extinction of outlying populations. As an outlier, *R. avalonense* lives a precarious existence under less than optimal conditions. Considered potentially vulnerable to extinction, protective status is warranted for this rare, insular endemic.

ARE *EUGLANDINA* AND *GONAXIS* EFFECTIVE AGENTS FOR BIOLOGICAL CONTROL OF THE GIANT AFRICAN SNAIL IN HAWAII?

Carl C. Christensen, Division of Malacology, Bernice P. Bishop Museum, Honolulu, Hawaii.

Frequent assertions have been made that the predatory snails *Euglandina rosea, Gonaxis kibweziensis,* and *G. quadrilateralis* have been demonstrated to be effective agents for the control of the giant African snail, *Achatina* *fulica.* Few of these statements have been based upon experimental evidence from systematically conducted field observations, however, and field studies conducted in Hawaii that have been cited in support of such claims do not adequately consider factors other than predation (particularly disease, parasitism, and reproductive seasonality) that may account for observations of decline in abundance of *Achatina* populations or that may influence the age distribution of those populations. As it has long been known that the abundance of *Achatina* in a particular locality may decline drastically in the absence of introduced predators, a finding that African snails became reduced in numbers following the introduction of predators does not prove the effectiveness of these predators as control agents unless a cause and effect relationship can be demonstrated between predation and the observed reduction in the abundance of *Achatina.* No compelling evidence has yet been presented that *Euglandina* and *Gonaxis* do in fact exert a meaningful level of control of pest snail populations in Hawaii. As the effectiveness of these predators as biological control agents is unproven, public health and agricultural authorities contemplating their introduction to additional Pacific Islands cannot assume that such introductions will yield health or economic benefits to offset the significant environmental costs that are likely to be associated with the establishment of these predators in fragile island ecosystems.

ANNUAL BUSINESS MEETING REPORT FOR 1983

The 49th annual business meeting of the American Malacological Union was called to order by President Alan J. Kohn at 8 p.m. in Room A of McCarty Hall, University of Washington campus, Seattle, Washington, on Thursday August 11, 1983. President Kohn announced that registration was 190. He said 91 papers and poster sessions were scheduled, with presenters from 24 states and four Canadian Provinces.

Minutes of the 1982 meeting, as published in the *Bulletin*, were approved.

Reports from officers and committees were summarized and approved and have been filed with the Recording Secretary. Membership and subscriptions for fiscal year 1982 totalled 787, an increase of 13. The Treasurer's report is printed below.

Of special interest was the report from Richard E. Petit, chairman of the Symposium Endowment Fund Committee, who announced that $10,500.00 had been accumulated for the fund as of August 1, 1983, and that this amount had been placed in certificates of deposit and money management funds. The continued solicitation of new funds, Chairman Petit envisioned, would result in the AMU Symposium Endowment Fund becoming self-sufficient in a few years.

Chairman Petit announced that $1,000 had been donated at this meeting by Dr. Louise Russert-Kraemer, and another $100.00 had been received from member Gary Rosenberg. He also announced that approximately $1,200.00 had been derived from the auction held during the meeting. This money goes into the Symposium Fund.

Commendation for the efforts by Mr. Petit in helping to establish the symposium fund and in handling the auction at this meeting were voted separately and unanimously approved.

Dr. Robert Prezant, Editor, asked members to help advertise the new *American Malacological Bulletin,* reporting that 1,200 copies of Volume I had been printed. This issue was mailed to members in July, 1983, and contained 140 pages, including six pages of errata. It cost $9,750.88. Volume II will be issued in early 1984. Volume III will have two numbers; No. 1 will be issued about July, 1984, and No. 2 is planned for December, 1984.

The budget voted for 1984 is as follows:

INCOME		
Memberships (except life and institutions)		$ 9,800.00
Sales		
HTSCS		300.00
Rare & End		10.00
Back Issues of *Bulletin*		400.00
Teskey Index		20.00
	SUBTOTAL SALES:	(730.00)
Page charges to authors		1,300.00
Proceeds of Meeting		1,500.00
Donations, Symposium		500.00
Miscellaneous		50.00
	TOTAL:	$13,880.00
Interest on savings (includes life members)		$ 1,151.19
DISBURSEMENTS		
Bulletin		$ 8,500.00
Newsletter		880.00
Conservation Committee		50.00
Membership Committee		125.00
President's organizing fund		500.00
California filing		7.50
Officers to Meeting		1,600.00
Legal Defense		50.00
Postage (minus *Bulletin* and Newsletters)		900.00
Printing (minus *Bulletin* and Newsletters)		200.00
Office Supplies		150.00
Postal Permit		

	45.00
Miscellaneous	450.00
Annual Meeting Expense	150.00
Advertisements of Meeting and HTSCS	500.00
Membership: WSM, ASC, etc.	45.00
Symposium Expense (1984 meeting)	500.00
Student Prize	250.00
TOTAL:	$14,902.50

SUMMARY

Income	$13,880.00
Interest on Savings	1,151.19 (includes life members int.)
Disbursements	14,902.50
Net gain	128.69

Dr. Robert Robertson reported that the next annual meeting, already approved for Norfolk, Virginia, will be held July 22–27, 1984, with headquarters at the Holiday Inn Scope Hotel. Featured symposia include one on Physiological Ecology of Freshwater Molluscs, to be organized by Drs. Albert Burky and Robert McMahon, which will honor Dr. W. D. Russell-Hunter. Another symposium is planned on the Larval Ecology of Mollusks to be organized by Dr. Michael Vecchione, with a workshop on collecting, studying, photographing and drawing veligers to be led by Dr. Jane Taylor. There will be a veliger field trip. Another workshop on the fossil and living mollusk faunas of Virginia and the Carolinas will be organized by Dr. R. Tucker Abbott. Midweek field trips will include a visit to the Rice Pit fossil locality at Hampton and a dredging trip to the mouth of the Chesapeake. Dr. Thomas Waller is slated to give a talk on pectens at the banquet. There will be an auction of shells and books.

Dr. Melbourne Carriker's plans to hold the 1985 meeting July 29–August 3 at the University of Rhode Island were approved.

Dr. Kohn summarized the report from Dr. Arthur Clarke, chairman of the AMU Conservation Committee, pointing out that this committee continues to monitor government activities on endangered species of mollusks. A survey has been conducted for two years on the critical habitat of a rare spiny mussel in the Tar River and adjacent drainages in North Carolina. This Fall there will be an assessment of the status of *Alasmidonta heterodon* in the upper Connecticut River System.

Changes in the AMU By-Laws approved follow:

ITEM I

Article I—Dues, Assessments, Fees

Article I, Section 4. Institutional and corporation subscription charges for the American Malacological Bulletin shall be as established by the Publication Committee.

ITEM II

Article III—Terms of Office and Duties of Council Members

Article III, Section 2, Subsection g. The Publications Editor shall be responsible for the editing and reproduction of all AMU publications. The Editor, President, Treasurer, and two Council members, as appointed by the President, shall comprise the Publications Committee to develop the format and content of AMU publications. The Editor will be the chairperson of the Publications Committee. They shall maintain records of printing and distribution costs, separately for each publication, and report on them annually to the Treasurer along with any requested estimate of future publication costs. The Publications Committee may recommend the undertaking of new AMU publications which shall require Council approval. Henceforth the official publication of the AMU shall be titled the American Malacological Bulletin.

ITEM III

Article VII—Use of Funds

Section 1. Funds, except as restricted in Article VII, Sections 2, 3, 4, and 5, consisting of the proceeds of membership dues, contribution of members, sales of publications, any annual earnings from these funds, or from whatever source, may be used in the general operation of the AMU. At the discretion of the Treasurer and with approval of the officers, the principal of these funds, except as prohibited in Article VII, Sections 2, 3, 4, and 5, may be used for financing regular AMU publications or for use in the general operations of the organization. At the discretion of the Council these funds may also be used in financing special publications. However, such a decision may only be reached during a regularly scheduled meeting of the Council.

Article VII—Restricted funds of the AMU

Section 2. A Symposium Endowment Fund is hereby established for the purposes of helping to defray necessary costs to present one or more symposia at the annual meeting. The principal is to be invested in a high-yield instrument and may not be invaded. Interest accrued in one year shall be available for use of the Symposia to be held the following year. The Treasurer shall inform the current President of the interest available from the preceding year. Any unused interest is to be added to the principal and thereafter considered to be part of the principal. The interest of the Symposium Endowment Fund shall be used for no other purpose.

Section 3. Additional Endowment Funds for specific purposes may be established by one or more donors with an initial minimum donation of $5,000.00. All such Endowment Funds must be approved by Council at a regularly scheduled meeting. The initial gift, and all subsequent additions to an Endowment Fund, shall be invested in an interest-bearing account that is segregated from operating funds. Interest earned by such an account normally shall be disbursed annually according to the terms of the original gift, or, if no awards are judged meritorious in a year, then it may accumulate for future awards.

The President shall appoint a three-member Endowment Review Committee which shall be responsible for the appropriate disbursement of all accured interest from the previous year. This Committee shall also direct the Treasurer to reinvest the principal amount of the Endowment Funds in whatever is deemed the most appropriate type of interest-bearing account. With the approval of the Council, an Endowment Fund may bear a name as recommended by the initial donor.

In the event that more than one Endowment Fund is established under these provisions, the same Endowment Review Committee may serve them all; however, the President may appoint separate committees. Neither the original donor nor any subsequent donor of $1,000.00 or more may serve on the Endowment Review Committee.

Section 4. The President shall be authorized to accept proposed gifts to the AMU which are to be used for specific purposes, but only if the conditions of the proposed gift are approved by a majority of the Executive Council. Approval may be obtained by mail or telephone. If the proposed gift is to be disbursed on a competitive basis, the President shall appoint a three-member Special Gifts Review Committee which will determine what awards are to be made. Neither the donor nor the donor's representative may serve on the Special Gifts Review Committee. The full amount of such gifts including accrued interest should be disbursed within two years of the time the funds are received.

Section 5. For purposes of increasing yield, principals of the Symposium Endowment Funds (Article VII, Section 2) and Special Endowment Funds (Article VII, Section 3) may be commingled in one or more investments, but they must be carried on the books as clearly separate entities with earnings of the commingled funds assigned proportionately in an annual accounting. They shall remain segregated from regular operating funds at all times.

A report indicated that the AMU Archives at the Academy of Natural Sciences of Philadelphia are housed in newly refurbished space and that they are growing. Curation of the valuable and extensive correspondence of Morris K. Jacobson has begun.

The following slate of officers was approved by acclamation:

President:	Robert Robertson (one year term)
President-Elect:	Melbourne Carriker (one year term)
Vice-President:	James Nybakken (one year term)
Corresponding Secretary:	Paula Mikkelsen (three year term)
Councillor-At-Large:	Paul Mikkelsen (two year term)
Councillor-At-Large:	Barry Roth (two year term)

Other officers in terms are as follows:

Recording Secretary:	Constance E. Boone (to 1985)
Treasurer:	Myra L. Taylor (to 1984)
Councillor-At-Large:	Carl W. Gugler (to 1984)
Councillor-At-Large:	Virginia Vail (to 1984)
Editor:	Robert S. Prezant

Dr. Kohn announced that there had been nine applications for the Bequaert Award, with the $400.00 grant going to graduate student Kenneth Emberton to continue his work on land snails. Several other applicants were most deserving, according to Dr. Kohn, who expressed regret that no other monies were available for grants.

Dr. George Davis reported on the meeting during this annual session of the AMU Council of Systematic Malacologists, stating that a report on how to look at inactive collections will be published by Dr. Shi-Kuei Wu. Standards to use for course work for graduate students are being developed. Plans on how to handle common names now being devised will be developed by the end of this year.

Dr. Kohn announced the resignation of Dr. David Stansbery as Chairman of the AMU Common Names Committee. The work of this committee was transferred earlier in the year to the AMU Council of Systematic Malacologists. Dr. Donna Turgeon acts as chairman of the Common Names Committee.

Other motions approved follow:

1. "The Treasurer will separate each of the named AMU funds in terms of principal and interest for the purpose of reporting to the Council and

members the funds pertaining to each function."

2. "The AMU will send special letters to AMU life members (who do not receive dues statements with new funds requests) seeking additional contributions."
3. "The incoming President is requested to find a legal counsel for AMU due to the resignation of H. Wallace Roberts who has moved to France."
4. "AMU requires submission of an abstract to be published in the *American Malacological Bulletin* by each individual presenting a paper at AMU, unless that paper presentation results in a full manuscript in the *American Malacological Bulletin.*"
5. "AMU requires a $15.00 fee for all contributed paper abstracts. A box will be placed on the Call for Papers to call attention to payment of this fee. This fee will be waived for bonafide students."
6. "The *American Malacological Bulletin* has first option for publishing any and all AMU Symposia."
7. "AMU membership dues will be raised, starting 1 January 1984, to $20.00, with the additional $5.00 permitting the Editor to produce two issues of the *American Malacological Bulletin,* or the equivalent in number of pages, per volume. The dues rate for bonafide students, however, will be $15.00."
8. "All motions passed by the Council will be posted in a public place at least six hours prior to the annual business meeting of the AMU."
9. "The interest, in perpetuity, of life membership money will be used for the publication fund."
10. "The Jack Parker Memorial Funds given to AMU will be used to support the AMU Archives."
11. "The incoming President shall appoint an individual identified as financial officer whose functions for the next year will be to chair a finance committee and to find monies for AMU."
12. "The auction chairman, Richad Petit, is authorized to dispose of unsold materials donated to AMU for the auction in a manner that will bring in the greatest amount of money for AMU."
13. "The AMU will join in the effort to sponsor the Mollusca section, at no financial cost to AMU, of a new information service that will provide current molluscan taxa literature citations, indexed by taxon, subject, and author, issued quarterly."
14. "The incoming President shall appoint a Constitution and By-Laws Committee to review and examine any and all matters and to bring recommendations to the next meeting."

Resolutions were presented from Council authorizing President Kohn to send letters of appreciation and commendation to Mr. Roberts for his years of service as legal counsel, to Paul Jennewein for his years of service as Corresponding Secretary, and to Dr. David Stansbery for his continued efforts over a period of years to develop plans for the common names of mollusks. These were unanimously approved separately.

A resolution of thanks was unanimously voted to the Pacific Northwest Shell Club for the generous donation of money to help support this meeting (raised by the shell quilt raffle).

A resolution of appreciation was unanimously approved to President Alan J.Kohn for his work in planning and executing this fine 1983 meeting.

Dr. Don Shasky rose to report that AMU's Honorary Life President S. Stillman Berry could not be present but that he is still well and in good spirits and in his 96th year.

A motion was approved unanimously to send greetings from this meeting to the honorary life president and those honorary life members who were not present.

Meeting was adjourned at 10 p.m.

Constance E. Boone, Recording Secretary

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1982

CHECK BOOK BALANCE, JANUARY 1, 1982			$ 8,261.54
RECEIPTS:			
Memberships:			
Regular	$ 4,191.00		
Life	180.00		
Sustaining	225.00		
Corresponding	346.00		
Clubs & Institutions, Domestic	911.00		
Clubs & Institutions, Foreign	272.00		
Subscriptions	205.00		
	6,330.00	6,330.00	
Sales:			
HOW TO STUDY & COLLECT SHELLS	240.15		
TESKEY INDEX	15.00		
RARE & ENDANGERED SPECIES	4.00		
AMU BULLETIN, Back Issues	405.00		
	664.15	664.15	
Other Receipts:			
Page Charges to Authors	967.00		
Memorials	842.00		
New Orleans Meeting	913.48		
New Orleans Auction	1,000.00		
Stamps & Card Sales	51.50		
Symposium Donations	485.00		
Endowment Fund Donations	2,775.00		
Re-deposit of Checks	29.00		
Miscellaneous	7.00		
	7,069.98	7,069.98	
TOTAL CASH ACCOUNTED FOR:		14,064.13	
TOTAL CASH HANDLED:			22,325.67
DISBURSEMENTS:			
AMU BULLETIN, Incl. postage, printing, etc.	$ 6,002.25		
AMU NEWSLETTER, Incl. postage, printing, etc.	873.24		
Other Postage	907.45		
Other Printing	182.10		
Office Supplies	163.09		
Dues and Advertising	57.50		
California Filing Fees	7.50		
New Orleans Meeting Expenses	333.09		
Student Award	250.00		
Conservation Committee	3.85		
Officers' Travel Expenses to Meeting	968.11		
Typewriter Repair	26.00		
Symposium Expenses	2,300.00		
Bank Charges and Returned Checks	64.50		
Refunds	13.00		
Zip Code Directory	9.00		

President Alan Kohn—Petty Cash	500.00		
Increase in Petty Cash for Recording Secretary	125.00		
Miscellaneous	187.43		
	12,973.11		
Endowment Fund Monies Deposited in Long Term Money Market Certificate	5,103.50		
Total Disbursements from All Activities	$18,076.61		
CHECK BOOK BALANCE, JANUARY 1, 1982			$ 8,261.54
TOTAL RECEIPTS			14,064.13
TOTAL CASH			22,325.67
TOTAL DISBURSEMENTS			18,076.61
CHECK BOOK BALANCE, DECEMBER 31, 1982			4,249.06
SASA* Savings Acct. #5-034514	$ 3,342.95		
Interest for 1982	189.00		
Total for Account	3,531.95		
SASA* Cert. of Deposit #22-906859	2,098.91		
Interest for 1982	377.76		
Total for Account	2,476.67		
SASA* Cert. of Deposit #5-906860 (Life Membership Fund)	3,247.12		
Interest for 1982	584.43		
Total for Account	3,831.55		
Endowment Fund Money Market Cert. #6300834-02, First Federal Savings Assoc.	5,103.50		
Interest for 1982	156.24		
Total for Account	5,259.74		

SASA* = San Antonio Savings Assoc.

RECAPITULATION OF ASSETS, DECEMBER 31, 1982:

Cash in Checking Acct., Mercantile Bank		$ 4,249.06	
Treasurer's Petty Cash		20.00	
Recording Secretary's Petty Cash		225.00	
President Alan Kohn's Petty Cash		500.00	
SASA* Acct. #5-034514		3,531.95	
SASA* Acct. #22-906859		2,476.67	
Endowment Fund Money Market Cert. #6300834-02		5,259.74	
		$16,262.42	
LIFE MEMBERSHIP ACCT. #5-906860	$ 3,831.55		
AMU NET WORTH, DECEMBER 31, 1982			$16,262.42
CHANGES IN CAPITAL ACCOUNT:			
AMU Capital Acct., January 1, 1982			14,048.40
AMU Capital Acct., December 31, 1982			16,262.42
NET INCREASE IN ASSETS			+ $ 2,214.02

Respectfully Submitted,
Myra L. Taylor, Treasurer

AMERICAN MALACOLOGICAL UNION, INC.
EXECUTIVE COUNCIL
1983–1984

OFFICERS

President .... Robert Robertson
President Elect .... Melbourne R. Carriker
Vice-President .... James Nybakken
Treasurer .... Myra L. Taylor
Recording Secretary .... Constance E. Boone
Corresponding Secretary .... Paula Mikkelsen
Bulletin Editor .... Robert S. Prezant
Councillors-At-Large .... Carl W. Gugler, Virginia Vail
Paul Mikkelsen, Barry Roth

PAST PRESIDENTS
(Current Members)

William J. Clench (1935)
Harald A. Rehder (1941)
Henry van der Schalie (1946–47)
A. Myra Keen (1948)
J. P. E. Morrison (1951)
A. Byron Leonard (1953)
Ruth D. Turner (1957)
R. Tucker Abbott (1959)
Thomas E. Pulley (1961)
William K. Emerson (1962)
Albert R. Mead (1963)
Juan J. Parodiz (1965)
Ralph W. Dexter (1966)
Arthur H. Clarke (1968)
Joseph Rosewater (1969)
Alan Solem (1970)
David H. Stansbery (1971)
Arthur S. Merrill (1972)
Dee S. Dundee (1973)
Harold D. Murray (1974)
Donald R. Moore (1975)
Dorothea S. Franzen (1976)
George M. Davis (1977)
Carol B. Stein (1978)
Clyde F. E. Roper (1980)
Richard S. Houbrick (1981)
Louise Russert-Kraemer (1982)
Alan J. Kohn (1983)

HONORARY LIFE PRESIDENT

S. Stillman Berry

HONORARY LIFE MEMBERS

R. Tucker Abbott
William J. Clench
A. Myra Keen
J. P. E. Morrison
Harald A. Rehder
Margaret C. Teskey
Ruth D. Turner
Henry van der Schalie

THE AMERICAN MALACOLOGICAL UNION MEMBERSHIP
(Revised October 17, 1983)

ABBOTT, DR. R. TUCKER, P. O. Box 2255, Melbourne, LA 32901.
AHLSTEDT, STEVEN, 11 E. Norris Rd., Norris, TN 37828 (Biological aide in Fisheries Management, TVA).
ALBERT, ERNEST AND BERNICE, 905 S. Bayshore Blvd., Safety Harbor, FL 33572.
ALEXANDER, ROBERT C., 423 Warwick Rd., Wynnewood, PA 19096.
ALLEN, JAMES E., 1108 Southampton Dr., Alexandria, LA 71301 (Tertiary micro-Mollusca).
ALLEN, DR. J. FRANCES, Rt. 2, Box 3039, Front Royal, VA 22630.
ALLEN, MISS LETHA S., 8 James St., Yarmouth, Nova Scotia, Canada B5A 2V1 (General collector).
AMARATUNGA, MR. TISSA, Dept. Fisheries and Oceans, Resource Branch, Box 550, Halifax, Nova Scotia, Canada B3J 2S7 (Life history, biology and management of cephalopods).
ANDERS, KIRK W., Shells of the Seas, Inc., P.O. Box 1418, Ft. Lauderdale, FL 33302 (Volutidae; all rare shells).
ANDERSON, CARLETON JAY, JR., 56 Kettle Creek Rd., Weston, CT 06883.
ANDERSON, ROLAND C., The Seattle Aquarium, Pier 59, Seattle WA 98101 (Invertebrate husbandry and natural history).
ANDREWS, DR. JEAN, 6615 LaConcha Pass, Austin, TX 78749.
ARDEN, GEORGE J., JR., 122 E. 38th ST., New York, NY 10016 (Cowries; effects of pollution on marine life in general).
ARMINGTON, STEWART AND LEE, 15932 Brewster Rd., Cleveland, OH 44112 (Shells with postage stamps and worldwide marine).
ASHBAUGH, KAREN, 9045 Comet St., El Paso, TX 79904.
ASHWELL, JAMES R., 2125 Mohawk Trail, Maitland, FL 32751 (General).
ATHEARN, HERBERT D., Museum of Fluviatile Mollusks, Rt. 5, Box 499, Cleveland, TN 37311 (Freshwater mollusks).
ATKINSON, DR. JAMES W., Dept. of Naural Science, Michigan State University, East Lansing, MI 48824 (Developmental biology; Terrestrial pulmonates—special emphasis on pattern formation in relation to spiral cleavage and gametogenesis—also evolutionary mechanisms which emerge from developmental events).
AUFFENBERG, KURT, Museum Technician, Florida State Museum, Univ. of Florida, Museum Rd., Gainesville, FL 32611 (Neritacea: Neritidae).
AVELLANET, MRS. HELENE, 105 Clpper Way, Fair Winds Villas, Nokomis, FL 33555.
AVILES, E., PROF. MIGUEL C., Apartado 6-765, Zona Postal El Dorado, Panama, Rep. of Panama (Histology and embryology).
BABRAKZAI, DR. NOORULLAH, Dept. of Biology, Central Missouri State Univ., Warrensburg, MO 64093.
BAERREIS, DAVID A., Box 4651 Beimer Ave., Taos, NM 87571 (Paleoecological interpretation through mollusks).
BAKER, MRS. HORACE B., 11 Chelton Rd., Havertown, PA 19083.
BAKER, NICHOLAS J., 285 Winter St., Weston, MA 02193 (U.S. East Coast and Caribbean collecting).
BANKSTON, DR. CECIL N., JR., 4841 Woodlake Dr., Baton Rouge, LA 70816 (Marine shell collector).
BARGAR, TOM AND DENISE SCHNEIDER-BARGAR, 1235 N. 7th St., Lincoln, NE 68508 (Functional morphology of gastropods).
BARLOW, MRS. G. BARTON (ALICE), 76 Westervelt Ave., Tenafly, NJ 07670.
BARRICK, MRS. TAMMY A., Rt. 10, Box 302, Hayward, WI 54843.
BATEMAN, JAMES R., P.O. Box 2036, Neptune City, NJ 07753 2036 (New Jersey shells, intertidal to 100 fms., also systematics of *Strombus* and *Cymatium,* worldwide distribution and variation).
BATTEN, DR. ROGER L., American Museum of Natural History, Central Park West at 79th St., New York, NY 10024 (Fossil and recent pleurotomarians).
BAUER, LAURA M., 2126 45th St., Galveston, TX 77550 (All mollusks).
BAUM, NEWMAN N., 83 Weaving Lane, Wantagh, NY 11793.
BAZATA, KENNETH R., 5440 Cleveland, Apt. 9, Lincoln, NE 68504 (Terrestrial pulmonates; *Dentalium*).
BEETLE, MS. DOROTHY E., Director, Patterson Planetarium, 2900 Woodruff Farm Rd., Columbus, GA 31907 (U.S. land and freshwater mollusks).
BERCOVITZ, ARDEN BRYAN, PHD, ℅ Research Dept., San Diego Zoo, P.O. Box 551, San Diego, CA 92112 (Reproductive biology and gonadal function).
BERGMANN, JOSEPH A., Rt. 3, Box 3064, Boerne, TX 78006 (Land and freshwater mollusks, recent and fossil).
BERMUDEZ, ALEJANDRO, P.O. Box 68, Missouri City, TX 77459 (*Murex* and nudibranchs from the Caribbean Zone).
BERRY, DR. ELMER G., 8506 Beech Tree Court, Bethesda, MD 20034.
BERRY, DR. S. STILLMAN, 1145 W. Highland Ave., Redlands, CA 92373.
BIANCHI, ANN, Box 235, Goodland, FL 33933.

BICKEL, DAVID, 613 West Ave. C., Bismarck, ND 58501 (Systematics and ecology of freshwater mollusks, esp. pleurocerid snails).

BIJUR, JEROME M., 135 Seventh Ave. N., Naples, FL 33940 (Buy, exchange Florida and Caribbean marine and Gulf of Mexico shells).

BIPPUS, EMMA LEAH, 2743 Sagamore Rd., Toledo, OH 43606 (Marine gastropods).

BISHOF, DAVID, 994 68th St. Ocean, Marathon, FL 33050.

BLACK, LUTHER F., School of Oceanography WB-10, Univ. of Washington, Seattle, WA 98195 (Deposit and suspension feeding biology and ecology).

BLAIR, LUCIANNE, 1033 Rockcreek Dr., Port Charotte, FL 33948.

BLAISTEN, DR. LIA O. B. DE, Nicolas San Juan 1535, Colonia del Valle, Mexico D.F., Mexico 03100 (Amateur scientist—American and Caribbean seashells; cowries and *Strombus*).

BLEAKNEY, DR. J. SHERMAN, Dept of Biology, Acadia Univ., Wolfville, Nova Scotia, Canada BOP 1XO (Nudibranchs, sacoglossans; ecology, zoogeography, systematics).

BLEDSOE, WILLIAM D., 352 Bon Hill Rd., Los Angeles, CA 90049.

BLOOM, JONATHAN A., RR6, Box 122, Town & Country TR CT., Carbondale, Il 62901 (Temporal changes in species diversity of freshwater mussels in Eastern U.S.).

BŌDY, RALPH L., 2538 10th Ave. W., Seattle, WA 98119 (Taxonomy).

BOGAN, ARTHUR E., Dept of Malacology, ANSP 19th and the Parkway, Philadelphia, PA 19103.

BOHLMANN, MISS URSULA C., #1121, 1030 South Park Street, Halifax, Nova Scotia B3H 2W3 Canada (Land and freshwater mollusks of North America; marine mollusks of Nova Scotia, Canada and West Africa).

BOONE, CONSTANCE E., 3706 Rice Boulevard, Houston, TX 77005.

BORRERO, FRANCISCO J., Dept. of Biology, Univ. of South Carolina, Columbia, SC 29208 (Ecology, population dynamics of bivalves, aquaculture of bivalves; taxonomy, ecology and distribution of mollusks, esp. from South American Pacific Coast (Columbia); coral-related Muricacea).

BORROR, KATHY GAIL, Museum of Zoology, OSU, 1813 N. High St., Columbus, OH 43210.

BOSS, DR. KENNETH JAY, MCZ, Harvard University, Cambridge, MA 02138.

BOWERS, RAYMOND E. and SYLVIA G., 128 E. Oakland Ave., Columbus, OH 43201 (Freshwater ecology of naiades.

BOYD, DR. AND MRS. EUGENE S., R #1, Box 549, Bokeelia, FL 33922 (All aspects of Phylum Mollusca).

BRAND, DR. TIMOTHY, 4130 38th St. #17, San Diego, CA 92015 (Eulimid gastropods parasitic on/in marine organisms).

BRANDAUER, MRS. NANCY E., 1760 Sunset Blvd., Boulder, CO 80302.

BRANSON, DR. BRANLEY A., P.O. Box 50, Eastern Kentucky Univ., Richmond, KY 40475.

BRATCHER, MRS. TWILA, 8121 Mulholland Terrace, Hollywood, CA 90046.

BRENCHLEY, DR. G. A. (GALYE), Assist. Prof., Dept. of Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92717 (Distribution, migration and experimental life history of mudsnails, *Ilyanassa obsoleta*).

BRITTON, DR. JOSEPH C., Dept. of Biology, Texas Christian University, Ft. Worth, TX 76129.

BROYLES, MRS. CATHERINE E., 5701 Fairfield Ave., Ft. Wayne, IN 46807.

BRUNSON, DR. ROYAL BRUCE, 1522 34th St., Missoula, MT 59801.

BUCHANAN, ALAN C., Missouti Dept. of Conservation, Fish & Wildlife Research Ctr., 1110 College Ave., Columbia, MO 65201 (Fisheries biologist).

BUCHER, ANITA P., 7504 Branchwood Dr., Mobile, AL 36609 (Taxonomy).

BUCKLEY, GEORGE D., 164 Renfrew St., Arlington, MA 02174.

BULLOCK, DR. ROBERT C., Dept of Zoology, Biological Sciences Bldg., Univ. of Rhode Island, Kingston, RI 02881 (Biology and systematics of the *Polyplacophora*).

BURCH, DR. JOHN B., Museum of Zoology, Univ. of Michigan, P.O. Box 2749, Ann Arbor, MI 48106 (Land and freshwater mollusks).

BURCH, MRS. JOHN Q., 1300 Mayfield Rd., Apt. 61-L, Seal Beach, CA 90740.

BURCH, DR. TOM AND MRS. BEATRICE L., P.O. Box 309, Kailua, HI 96734 (BLB, planktonic mollusks; TAB, deepwater mollusks).

BURGER, SYBIL B., 3700 General Patch N.E., Albuquerque, NM 87111 (Gulf of Mexico and land snails).

BURKE, MRS. PATRICIA, 18128 Lakeside Lane, Nassau Bay, TX 77058.

BURKY, DR. ALBERT J., Dept. of Biology, Univ. of Dayton, Dayton, OH 45469.

BUROKER, DR. NORMAN E., Bur. of Biological Research, P.O. Box 1059, Rutgers, The State Univ. of New Jersey, Piscataway, NJ 08854 (Evolutionary and population genetics of pelecypods).

BUTLER, NANCY M., Dept. of EPO Biology, Univ. of Colorado, Boulder, CO 80309.

CAKE, DR. EDWIN W., JR., Head, Oyster Biology Sect., Gulf Coast Res. Lab., East Beach, Ocean Springs, MS 39564 (Oysters, Cestode parasites of marine mollusks, mariculture of estuarine mollusks).

CALDWELL, DR. RONALD S., Dept. of Biology, Texas College, Tyler, TX 75701 (Terrestrial gastropods of Kentucky).

CALL, SAM M., 107 Goodrich Ave., Lexington, KY 40503 (Pelecypods).

CAMPBELL, MR. and MRS. DONALD C., 3895 DuPont Circle, Jacksonville, FL 32205 (General collecting).

CAMPBELL, DR. LYLE D., 126 Greengate Lane, Spartanburg, SC 29302 (Tertiary mollusks, Eastern U.S.A.; marine mollusks, Western Atlantic; systematics, ecology, zoogeography).

CAPO, THOMAS R., 59 Nickerson St., E. Falmouth, MA 02536 (Benthic ecology).

CARLTON, DR. JAMES T., Mystic Seaport Museum, Mystic, CT 06355 (Estuarine and brackish water mollusks).

CARNEY, CDR. W. PATRICK, MSC USN, 12900 Turnbrook Parkway, Rockville, Md 20851.

CARRIKER, PROF. MELBOURNE R., College of Marine Studies, Univ. of Delaware, Lewes, DE 19958.

CARSON, JOHN and LAURA W., 221 Elm Ave., Morrisville, PA 19067.

CASTAGNA, MICHAEL, Virginia Institute of Marine Science, Wachapreague, VA 23480 (Pelecypod larval behavior).

CASTIGLIONE, MS. MARIE C., 5832 S. Alameda, Apt. C., Corpus Christi, TX 78412 (Gulf of Mexico mollusks).

CATE, MRS. CRAWFORD N. (Jean M.), P.O. Box 3049, Rancho Santa Fe, CA 92067 (*Mitra, Cypraea*; no exchanges).

CHADWICK, ALBERT F., 2607 Turner Rd., Wilmington, DE 19803 (Marine shells).

CHALERMWAT, MR. KASHANE, P.O. Box 7240, University of Southern Mississippi, Hattiesburg, MS 39406 (Molluscan developmental biology).

CHAMBERS, DR. STEVEN M., OES, U.S. Fish & Wildlife Service, Dept. of the Interior, Washington, DC 20240.

CHANLEY, MR. and MRS. PAUL, P.O. Box 12, Grant, FL 32949.

CHICHESTER, LYLE F., Dept. of Biological Sciences, Central Conn. State College, 31 Chamberlain St., New Britain, CT 06052 (Ecology of terrestrial gastropods, biology of land slugs).

CHRISTENSEN, CARL C., Bernice P. Bishop Museum, P.O. Box 19000-A, Honolulu, HI 96819.

CHRISTIE, DR. JOHN D., Dept. of Pathology, Univ. of Texas Medical Banch, Galveston, TX 77550.

CHROSCIECHOWSKI, PRZEMYSLAW K., APTDO 125, Maracay, Venezuela 2101 A (Planorbidae).

CHUNG, DANIEL, Museum of Zoology, Univ. of Michigan, Ann Arbor, MI 48104 (Pulmonates; Hawaiian mollusks).

CICERELLO, RONALD R., Aquatic biologist, Kentucky Nature Preserves Commission, 407 Broadway, Frankfort, KY 40601.

CLARK, DR. KERRY B., Dept of Biological Sciences, Florida Institute of Technology, Melbourne, FL 32901 (Opisthobranchs).

CLARKE, DR. ARTHUR H., Ecosearch, Inc., 7 Hawthorn St., Mattapoisett, MA 02739.

CLENCH, DR. WILLIAM J., 26 Rowena St., Dorchester, MA 02124 (Land shells in all of the West Indies—freshwater mollusks in North America).

CLOVER, PHILLIP W., P.O. Box 83, Glen Ellen, CA 95442 (Rare *Cypraea, Conus, Voluta, Murex* and *Marginella*; buy and exchange).

CLYMER, GEORGE M., Midwest Trailer Court, Lot #24, Hutchinson, MN 55350 (Unionids).

COAN, DR. EUGENE V., 891 San Jude Ave., Palo Alto, CA 94306.

COLE, DR. TIMOTHY JAMES, Horn Point Environmental Lab., Univ. of Maryland, Box 775, Cambridge, MD 21613 (Genetic divergence among molluscan populations; ecological-genetic interdigitations).

COLEMAN, DR. RICHARD W., Dept. of Biology, Upper Iowa University, Fayette, IA 52142 (Environmental interrelationships; plants, invertebrates.

COMPITELLO, MRS. JULIETTE, 5630 Alta Vista Road, Bethesda, MD 20034.

COOK, BUNNIE AND GEORGE, 1120 Makaiwa St., Honolulu, HI 96816 (Marine—Mitridae and other families).

COOK, DR. SUSAN B., The Bunting Institute of Radcliffe College, 10 Garden St., Cambridge, MA 02138 (Behavioral ecology of tropical marine gastropods; behavioral ecology of freshwater gastropods).

COOPER, ROBERT W., 5012 Pfeiffer Rd., Peoria, IL 61607 (Florida marine: world *Murex, Pecten, Spondylus*; Scuba).

COOVERT, GARY A., 36 Prospect Ave., Dayton, OH 45415 (Taxonomy of worldwide mollusca; esp. Pectinidae).

CONEY, C. CLIFF, Dept. of Biology, Coastal Carolina College, Univ. of South Carolina, Conway, SC 29526 (Evolutionary biology of terrestrial and freshwater mollusks).

CORGAN, DR. JAMES X., Dept. of Geology, Austin Peay State Univ., Clarksville, TN 37040 (Pyramidellidae, Vitrinellidae, scaphopods, Tertiary faunas.

CORPUZ, GLADYS C., Dept. of Zoology, University of Hawaii, Honolulu, HI 96822 (Life history and ecology).

COSMAN, DIETER, 3051 State Road 84, Ft. Lauderdale, FL 33312 (Marine tropical and subtropical Gastropoda and Bivalvia worldwide).

CRAMER, FRANCES L., 766 Obispo Ave., Long Beach, CA 90804 (Ecology; conservation).

CRISSINGER, MYRNA MAY and WILLIAM (BILL), 820 North Court St., Crown Point, IN 46307.

CROFT, MRS. THOMAS L., Box 7, Captiva, FL 33924 (Marine; fossils).

CUTLER, JIM, Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577.

CUMMINGS, RAYMOND W., 37 Lynacres Blvd., Fayetteville, NY 13066 (Shells from the West Indies, esp. Windward and Grenadine Islands).

CUMMINS, HAYS, Dept. of Oceanograpy, Biology Section, Texas A. & M. University, College Station, TX 77843 (Benthic ecology).

CUTLER, HENRY H., 105 Abbott Rd., Wellesley Hills, MA 02181.
DANFORTH, LOUISE L., 1241 Lake Ave., Apt. D, Metaire, LA 70005.
DARCY, GEORGE H., 17911 SW 92 Ct., Miami, FL 33157.
D'ASARO, CHARLES N., University of West Florida, Pensacola, FL 32504 (Reproduction and development of prosobranchs).
DAVENPORT, LILLIAN B. and John W., 802 Cape Ave., Box 81, Cape May Point, NJ 08212 (Conchology, malacology, anything about the sea).
DAVIS, DR. DEREK S., Nova Scotia Museum, 1747 Summer St., Halifax, Nova Scotia, Canada B3M 3A6 (Gastropod biology and taxonomy).
DAVIS, DR. GEORGE M., Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, PA 19103.
DAVIS, DR. JOHN D., 25 Old Homestead Rd., P.O. Box 156, Westford, MA 01886 (Ecology of marine bivalves).
DEATRICK, PAUL A., 218 SW 32 Ave., Miami, FL 33135 (*Strombus, Busycon*).
DE GRAAFF, GERRIT, 10915 SW 55 St., Miami, FL 33165.
DEISLER, JANE E., Dept. of General Biology, Univ. of Arizona, Tucson, AZ 85721 (Systematics of land snails).
DEMOND, MISS JOAN, 202 Bicknell Ave. #8, Santa Monica, CA 90405.
DEUEL, MR. and MRS. GLEN A., 8011 Camille Drive, Huntsville, AL 35802 (Microscopic seashells).
DEXTER, DR. RALPH W., Dept. of Biological Sciences, Kent State Univ., Kent, OH 44242.
DEYNZER, ALBERT E. and BEVERLY A., Showcase Shells, 1614 Periwinkle Way, Sanibel, FL 33957 (Marine mollusks).
DEYRUP-OLSEN, DR. INGRITH, Dept. of Zoology, NJ-15, Univ. of Washington, Seattle, WA 98195 (Physiology of fluid exchange; mucus formation).
DIETRICH, MRS. LOUIS E. (GERTRUDE B.), 308 Veri Drive, Pittsburgh, PA 15220.
DILLON, ROBERT T., JR., Dept. of Biology, College of Charleston, Charleston, SC 29424.
DIMATTEO, TONY, #U-5824, Tallahassee, FL 32313 (Opisthobranch and gastropod defensive mechanisms, predator-prey interactions).
DRAPER, BERTRAM C., 8511 Bleriot, Los Angeles, CA 90045 (Eastern Pacific minute mollusks and all Western U.S. marine mollusks).
DUBAR, DR. AND MRS. JULES R., 12600 Esplanade St., Austin, TX 78758 (Cenozoic and recent mollusks; ecology and paleoecology).
DUNDEE, DR. DEE, Dept. of Biological Sciences, Univ. of New Orleans, Lakefront; New Orleans, LA 70148 (Land mollusks; freshwater mussels).
DUSHANE, HELEN, 15012 El Soneto Drive, Whittier, CA 90605 (Worldwide Epitoniidae).
DVORAK, STANLEY J., 3856 W. 26th St., Chicago, IL 60623 (Muricidae).
EDDISON, GRACE G., M.D., "Wildwood," Rt. 4, Carlisle, KY 40311.
EDWARDS, MS. AMY LYN, P.O. Box 13687, Savannah, GA 31406 (Atlantic marine mollusks).
EDWARDS, D. CRAIG, Dept. of Zoology, Morrill Science Center, University of Mass., Amherst, MA 01003–0027 (Population ecology and behavior of marine benthic mollusks).
EMBERTON, KENNETH C., ELLEN AND LUCIA, 6044 S. Ingleside I-N, Chicago, IL 60637 (Land snails).
EMERSON, DR. WILLIAM K., American Museum of Natural History, Central Park West at 79th St., New York, NY 10024.
ENG, DR. LARRY L., 1701 Nimbus Rd., Suite "C," Rancho Cordova, CA 95670.
ERICKSON, CARL W., 4 Windsor Ave., Auburn, MA 01501.
ERICKSON, RICHARD J., P.O. Box 52920, Tulsa OK 74152-0920 (Tertiary mollusca, recent Gulf of Mexico).
EUBANKS, DR. ELIZABETH R., 57 Lyall St., West Roxbury, MA 02132 (Florida marine shells).
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PEARCE, DR. JOHN B., NOAA, NMFS, Northeast Fisheries Center, Sandy Hook Laboratory, Highlands, NJ 07732 (Symbiotic relationships of crustacean (pinnotherid crabs) with mollusks; the role of mollusks in benthic communities).

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In Errata: Volume 1 page 103, Dr. Louise R. Kraemer was instrumental in organizing the Second International Symposium on Molluscan Genetics at A.M.U. 1982.

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Cover. The aboreal snail *Liguus fasciatus* of Florida and Cuba shows wide variations in shell color and patterning. Two such forms are shown on the cover. For full details see paper in this volume by Roth and Bogan, pages 1–10.

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SHELL COLOR AND BANDING PARAMETERS OF THE *LIGUUS FASCIATUS* PHENOTYPE (MOLLUSCA: PULMONATA)

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ABSTRACT

The arboreal snail *Liguus fasciatus* of Florida and Cuba shows great variety in shell color and patterning. The existing taxonomy, based on total phenotype considered typologically, has contributed to a view of its evolution and zoogeography that relies heavily on migration, multiple dispersal events, and hybridization of so-called "pure" races.

Elements of shell color and pattern appear to inherit separately and can be expressed by an alphabetic code. Most character-states are widely distributed throughout the Floridian range of the species. The highest character-state diversity is clustered in the Pinecrest area and on the Atlantic coastal ridge.

A model of *Liguus* biogeography based on the fragmentation of an originally widespread, homogeneous, and phenotypically diverse population is proposed, in contrast to the traditional model of random dispersal by hurricane. It is supported by previous studies of color morph diversity and by the regional trend shown here.

The arboreal pulmonate snail *Liguus fasciatus* (Müller, 1774) of Cuba and southern Florida displays great variety in shell color, banding, and maculation. From the nineteenth century to the present, conchologists have delighted in naming the many attractive color forms. About 58 nominal forms are now recognized in Florida (Clench, 1946, 1954, 1965; Pilsbry, 1946; Davidson, 1965; Jones, 1979; Deisler, 1982), and perhaps 44 in Cuba (Clench, 1946, 1954, 1965). Opinions vary as to synonymy, but most of the names continue to be used to designate infrasubspecific "forms" and "varieties." As in the case of similarly polymorphic species such as *Cepaea nemoralis* (Linnaeus, 1758) (see Cain and Currey, 1963; Murray, 1975) and *Littorina saxatilis* (Olivi, 1792) (see Pettitt, 1973), the varietal names may or may not specify details of color or banding. More often they commemorate people or places or a general appreciation of the phenotype (e.g. *spendidus, delicatus*). While they may be perfectly intelligible to a specialist who has already memorized an image or series of images to go with a particular name, in practice these eipithets tend to obscure rather than illuminate the relationship of one form to another. In addition, as we hope to show, their use has canalized systematic and zoogeographic thought regarding the genus *Liguus*.

HISTORICAL

A brief history of the classification of *L. fasciatus* color forms will show how the present system of nomenclature developed. Pilsbry (1899) defined ten major and eight minor color forms among Cuban and Floridian populations, leaving most unnamed below the species level but applying preexisting names (*L. f. crenatus* Swainson, *L. f. solida* Say), when available, for "varieties." He cited 12 Florida localities from Key West to Miami and Goodland Point, briefly characterizing the color forms known to be present at each. Later, in a study of Florida *Liguus*, Pilsbry (1912) recognized what he called five "leading races," designated as *L. solidus, L. crenatus, L. fasciatus lignumvitae, L. f. roseatus,* and *L. f. castaneozonatus.* He stated that colonies consisting solely of one such form were pure "by virtue of their isolation" (p. 432); hence, heterogeneous colonies were the result of secondary

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mingling and hybridization between pure races. This view led him to express "hybrid" morphologies by complex terminology: "*Liguus crenatus* × *roseatus* × *castaneozonatus* × *testudineus*" (Pilsbry, 1912, pl. 39, Figs. 22–22h), and so forth. He did admit a certain amount of variability within the "leading races" and designated the chief variants by additional infraspecific names. He proposed (1912, p. 434) a simple formula in which capital and lower-case letters stood for the presence and absence, respectively, of various color factors (G, g, green lines; R, r, rose coloring; Y, y, yellow coloring, etc) but did not exploit the potential of such a system for characterizing the distribution of these factors over the range of the species.

Simpson (1929) recognized 32 subspecies of Florida *Liguus*, allocated to three species—*L. crenatus, L. fasciatus*, and *L. solidus*—and cited localities for all. Simpson's subspecies were not geographic entities. He reported thirteen from one large hammock at Miami and many other cases of sympatry. Like Pilsbry, Simpson took a dispersalist view of *Liguus* history, invoking migration and multiple dispersal events to account for the deployment of these taxa.

Clench and Fairchild's (1939) outline classification arranged all Florida *Liguus* under three subspecies of *L. fasciatus*—*L. f. solidus, L. f. lignumvitae*, and *L. f. roseatus*—with seven to nineteen named "forms" under each. The subspecies were geographically delimited, *L. f. solidus* from the lower Florida Keys (No Name Key to Key West), *L. f. lignumvitae* from "the lower keys of the upper series," and *L. f. roseatus* from the mainland and the upper keys as far south as Upper Matecumbe Key. Whereas earlier authors had championed the presence of more than one species in Florida, even while acknowledging liberal interbreeding between them, Clench and Fairchild (1939, p. 78) stated, "Only one species occurs in Florida, that of *Liguus fasciatus* Mull., which has broken up into several subspecies . . . ." They also noted the probable role of recombination of characters in bringing about parallelism.

Clench (1942, p. 71) again emphasized parallelism in similar color forms, "not related *inter se* but . . . directly related to the differently colored forms in their own locality." De la Torre (1938) observed that an unpigmented shell could occur in all species and varieties of the genus.

Pilsbry (1946) criticized Clench and Fairchild's (1939) system for admitting too much variation within a subspecies, and proposed instead a nested hierarchy of names. Abandoning the geographic concept of subspecies (to which he generally adhered elsewhere to his monograph of North American land Mollusca), he assigned subspecific rank to eight "really different races." "In any subspecies the color may vary from fully developed to albinistic. . . . The chief stages in this scale of color patterns are distinguished as *Forms*. In most cases the 'form' is characterized by peculiarities of pattern, often by loss of some color factor. Subordinate to the 'forms' are placed numerous minor strains here called *Varieties*, many of them intergrading freely, being selected stages of clines . . . " (Pilsbry, 1946, p. 41). A list of color forms from a single hammock at Miami included nine infraspecific taxa, belonging to five "subspecies" of Pilsbry's general classification. Other locality lists show equivalent sympatry of the "really different races;" indeed, several were recorded from the same clutch of eggs. With minor variations of opinion (e.g., Close, 1978) the Pilsbryan system of nomenclature has been adopted by most later workers.

Young (1960) noted that the occurrence of distinctive variants in pure colonies suggests that basic shell pattern and pigmentation are directly controlled by relatively few genes. He regarded colored apex and columella, peripheral banding, sutural banding, yellow pigments, dark pigments, brown or brownish-red peripheral or sutural lines or both, and periostracal green lines as probably representing unit characters, and briefly employed a seven-digit formula to express the presence or absence of these factors in several of the named varieties.

Rex's (1972) study, the first to test the relation between the deployment of color forms and environmental factors, found that at Long Pine Key, hammock area was a good predictor and isolation a poor predictor of the number of sympatric color varieties. He recognized nine morphotypes and used names from Pilsbry (1946).

Under the Pilsbryan system, although it is recognized that elements of color and pattern inherit separately, names are given total phenotypes; and once named, these taxa are treated as if they were monophyletic units—individuals, not classes. An example is Pilsbry's (1946, p. 41) definition, quoted above, of his varieties as *strains* (i.e. hereditary lines). This assumption or prejudice underlines the dispersal-laden zoogeography of Pilsbry (1912, 1946) and Simpson (1929). For reasons that are never made clear, Pilsbry rejected the effect of selection in determining color morph distribution (although he wrote of "loss of one or more components of the color pattern . . . [in] all of the main stocks" [1946, p. 49]) and emphasized the founder effect in determining composition of colonies (p. 45).

By contrast, the recognition of parallelism through the independent association of characters (Clench, 1942; Clench and Fairchild, 1939) implies the existence of a rich and originally widespread pool of genetic diversity which has been more or less disrupted by factors of isolation and selection. "Pure" colonies are therefore not necessarily archetypal, as in the Pilsbryan model, but special cases of reduced population heterogeneity; "hybrid" colonies, the bugbear of Pilsbryan nomenclature and zoogeography, possibly retain more of the variability that may once have been general. The virtue of this second model is that it admits testing for correlation with environmental variables and the search for agents of selection.

It is true that color and pattern are not the only features involved in the definition of "forms;" shape and texture are apparently quite informative to specialists (Close, 1978; De la Torre, 1938) and may illuminate the history of *Liguus* evolution as well. The purpose of this paper is not to judge the validity of subspecific or any other ranking for any of the nominal taxa now recognized, but rather to suggest that the study of color variation and inheritance in *Liguus* be pursued independent of the strictures of a nomenclature based on total phenotype. Toward this goal we propose a system that designates the individual characters and not (as in the present nomenclature) just the morphotypes that result from their numerous combinations.

What all authors have really been observing is the distribution of various character-states and, presumably, their underlying alleles or allelic combinations. Inheritance of these states is probably particulate (perhaps modified by a yet undetermined number of linkages), but the details of the genetic system will not be known until analyzed by breeding experiments.

The idea of a code or formula for analysis of color vaiation in *Liguus* is not new with us; it is anticipated in the formulae proposed—but not really pursued—by Pilsbry (1912) and Young (1960).

MATERIAL EXAMINED

Material examined includes the *Liguus* collections of the Academy of Natural Sciences of Philadelphia (ANSP) and the California Academy of Sciences (CAS). At least one lot of every nominal taxon was seen. The descriptive literature was examined for illustrations of additional morphotypes not represented in these collections. The characters used here are ones in which the alternative states can be seen to segregate in randomly selected material. Most museum lots were sorted by earlier workers to conform to the standard nomenclature and cannot be used to determine whether a particular variation is discontinuous or not.

NOTATION

The notation proposed here (Table 1) is modeled after systems now in use for *Cepaea* (Cain, Sheppard, and King, 1968; Murray, 1975), *Littorina* (Pettitt, 1973), and *Monadenia* (Roth, 1981). The system may be conceived as a multidimensional array representing the combinations of character-states that define all theoretically possible morphotypes. The letters designating shell color and banding parameters resemble, in part, the set for *Cepaea* (Murray, 1975), but *Liguus* and *Cepaea* are so distantly related that no homology is implied.

Ground color (C) is given (Table 1) as a two-state character (yellow or white), but if distinct subclasses of yellow pigmentation were recognized, they could be recorded with an additional superscript: C^{Y1}, C^{Y2}, etc. The basic banding motif consists of a pair of broad spiral bands separated at the periphery by a zone of ground color (Figs. 1, 6); the ground color also appears below the suture and around the columella. Pilsbry (1946) called this the "*dryas*" pattern. The *dryas* bands (B) are brown or yellow; often both pigments are present in superimposition, the yellow detectable through gaps in the brown. The pigment may spread (S) beyond the limits of the *dryas* bands, more or less covering the ground color except in the region of the columella (Fig. 2). Even the least spread-banded specimens segregate from those without spreading. It is rare for the two bands to fuse completely; even the most thoroughly spread-banded shells show a narrow light zone at the periphery (Fig. 3; compare Pilsbry, 1946, Figs. 38e–h).

Table 1. Notation for scoring shell color and pattern in *Liguus fasciatus*

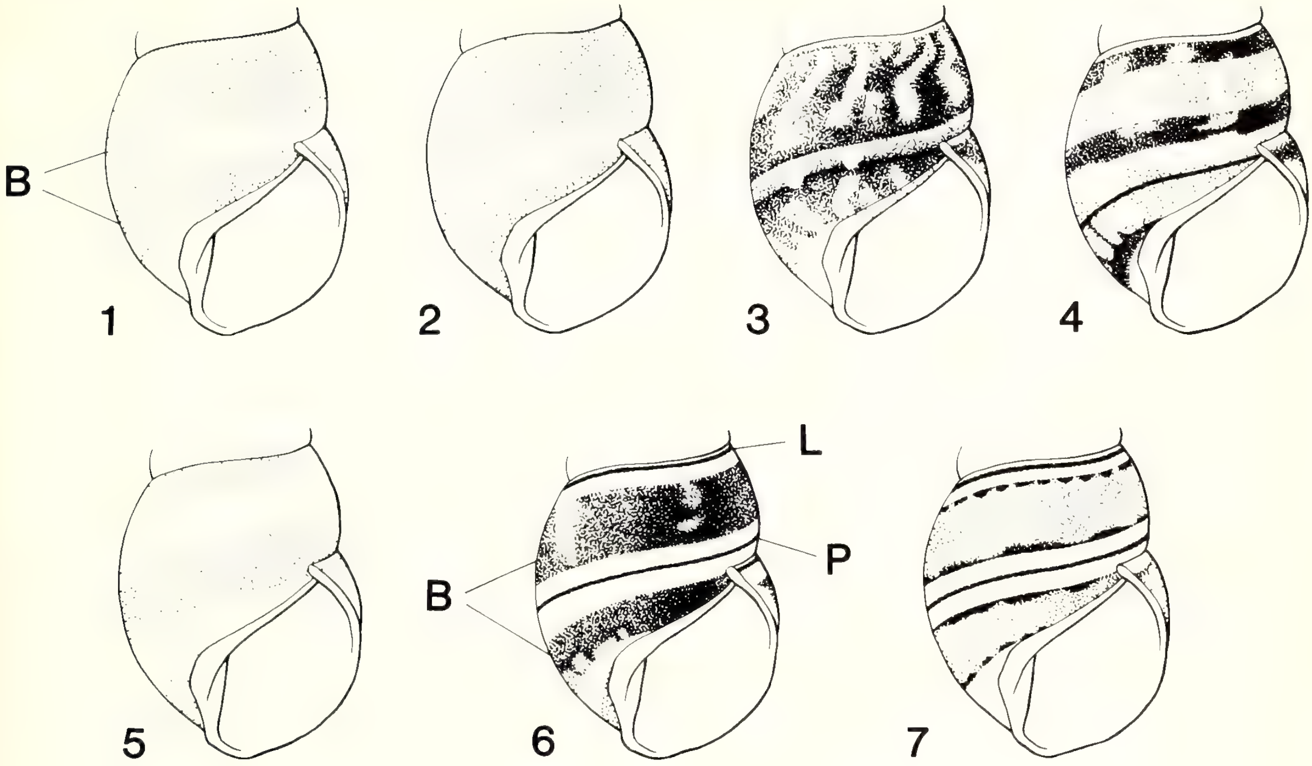
C	Ground color of shell	C^Y yellow; C^W white
B	Presence or absence of *dryas* bands	B^B present, brown; B^Y present, yellow; B^{BY} both brown and yellow present; B^O absent
S	Spreading of *dryas* band pigment	
E	Vacant center of *dryas* bands	E^B center of brown band vacant; E^Y center of yellow band vacant; E^{BY} center of both brown and yellow vacant
U	Absence of one *dryas* band	U^U upper band absent; U^L lower band absent
M	Marbling of *dryas* bands	
L	Sutural line	L^B present, brown; L^Y present, yellow; L^P present, pink; L^O absent
P	Peripheral line	P^B present, brown; P^Y present, yellow; P^P present, pink; P^O absent
A	Pink apex	
O	Pink columella	
W	White suffusion	
G	Periostracal green lines	

Pigment may be confined to the edges of the *dryas* bands, their centers being vacant (E) (Fig. 4); where both brown and yellow pigments are present, this condition may affect one or the other or both. A "negative-*dryas*" pattern (Fig. 5) is found, probably resulting from a combination of vacant band centers and the spread-banded condition. Either the upper or the lower *dryas* band may be absent (U). The band pigment may be marbled longitudinally (M) (Figs. 3, 4). Many specimens show variation in pigment density correlated with seasonal increments of shell growth, somewhat as reported in *Monadenia fidelis* (Roth, 1981), while other forms of marbling cut across growth lines and are probably unrelated to nutrition or time of year. At their first appearance, on whorls three and four, the *dryas* bands seem always to be regularly marbled longitudinally. Marbling in the adult shell may prove to be a paedomorphic condition as in *Poecilozonites* (Gould, 1969). In Table 2, where named infraspecific taxa of Florida *Liguus fasciatus* are scored for the various parameters defined here, the notation "M" is applied only to forms showing regular, non-seasonal, marbling.

A form of marbling consisting of narrow axial flammules of brown on a yellowish ground, seen in the varieties *L. f. alternatus* and *L. f. fuscoflamellus*, may prove to require a designation of its own. In many forms a condition occurs resembling that called "punctate" in *Cepaea*, wherein narrow spiral bands are interrupted into rows of dots (Fig. 7). This seems to result from a combination of marbling and vacant band centers.

Table 2. Notation of morphotypes included in named infraspecific taxa of *Liguus fasciatus* in Florida.

Nominal taxon	Morphotypes
alternatus Simpson, 1920	$C^{W}B^{BY}ML^{B}P^{B}AO$, $C^{W}B^{BY}ML^{O}P^{O}AO$
aurantius Clench, 1929	$C^{Y}B^{Y}SE^{Y}L^{O}P^{O}G$, $C^{Y}B^{Y}L^{O}P^{O}G$
barbouri Clench, 1929	$C^{Y}B^{BY}SML^{B}P^{B}WG$, $C^{Y}B^{BY}SE^{B}ML^{B}P^{B}WG$
beardi Jones, 1979	$C^{Y}B^{B}U^{U}ML^{B}P^{B}AG$
capensis Simpson, 1920	$C^{W}B^{O}L^{O}P^{O}G$, $C^{W}B^{Y}U^{L}L^{O}P^{O}G$
castaneozonatus Pilsbry, 1912	$C^{W}B^{BY}L^{B}P^{B}AOG$, $C^{W}B^{BY}E^{B}L^{B}P^{B}AOG$, $C^{W}B^{BY}E^{B}U^{L}L^{B}P^{B}AOG$
castaneus Simpson, 1920	$C^{Y}B^{B}SML^{B}P^{B}AO$, $C^{Y}B^{B}SML^{B}P^{B}A$, $C^{Y}B^{B}SML^{B}P^{B}O$
cingulatus Simpson, 1920	$C^{W}B^{Y}L^{O}P^{O}$, $C^{W}B^{Y}L^{O}P^{Y}$, $C^{W}B^{Y}L^{O}P^{O}G$, $C^{W}B^{Y}L^{O}P^{Y}G$
clenchi Frampton, 1932	$C^{Y}B^{Y}SE^{B}ML^{O}P^{O}AOG$, $C^{Y}B^{B}SE^{B}ML^{O}P^{O}AOWG$
crassus Simpson, 1920	$C^{W}B^{O}L^{O}P^{O}G$
deckerti Clench, 1935	$C^{W}B^{BY}L^{B}P^{B}G$
delicatus Simpson, 1920	$C^{W}B^{Y}L^{B}P^{B}AOG$, $C^{W}B^{BY}E^{B}U^{L}ML^{B}P^{B}AOG$
dohertyi Pflueger, 1934	$C^{Y}B^{Y}SE^{B}ML^{B}P^{B}AWG$
dryas Pilsbry, 1932	$C^{W}B^{Y}L^{Y}P^{Y}AO$, $C^{W}B^{Y}L^{Y}P^{O}AO$
eburneus Simpson, 1920	$C^{W}B^{O}L^{O}P^{O}G$
elegans Simpson, 1920	$C^{W}B^{O}L^{B}P^{B}AOG$
elliottensis Pilsbry, 1912	$C^{W}B^{O}L^{Y}P^{O}G$, $C^{W}B^{O}L^{O}P^{O}G$
evergladensensis Jones, 1979	$C^{Y}B^{BY}E^{B}ML^{B}P^{B}AOWG$
farnumi Clench, 1929	$C^{W}B^{BY}SE^{B}ML^{O}P^{B}G$
floridanus Clench, 1929	$C^{Y}B^{BY}SE^{B}ML^{O}P^{B}G$, $C^{W}B^{BY}SE^{B}ML^{O}P^{B}G$
framptoni Jones, 1979	$C^{W}B^{B}E^{B}ML^{O}P^{O}AOG$, $C^{W}B^{B}E^{B}ML^{O}P^{B}AOG$
fuscoflamellus Frampton, 1932	$C^{W}B^{BY}SE^{B}ML^{B}P^{B}G$
gloriasylvaticus Doe, 1937	$C^{W}B^{BY}SE^{BY}ML^{B}P^{B}G$
graphicus Pilsbry, 1912	$C^{W}B^{BY}E^{B}ML^{B}P^{B}AOW$
humesi Jones, 1979	$C^{Y}B^{B}SML^{O}P^{O}AG$, $C^{Y}B^{B}ML^{O}P^{O}AOG$
innominatus Pilsbry, 1930	$C^{W}B^{BY}E^{B}ML^{B}P^{B}AOW$, $C^{W}B^{BY}ML^{B}P^{B}AOW$
kennethi Jones, 1979	$C^{W}B^{BY}SML^{B}P^{B}G$, $C^{W}B^{BY}SML^{B}P^{B}$
lignumvitae Pilsbry, 1912	$C^{W}B^{B}E^{B}ML^{B}P^{B}AOWG$, $C^{W}B^{BY}E^{B}ML^{B}P^{B}AOWG$
lineolatus Simpson, 1920	$C^{W}B^{Y}L^{P}P^{P}AOG$, $C^{W}B^{Y}L^{P}P^{Y}AOG$
livingstoni Simpson, 1920	$C^{W}B^{Y}L^{O}P^{O}AOG$, $C^{W}B^{Y}L^{B}P^{O}AOG$
lossmanicus Pilsbry, 1912	$C^{Y}B^{O}L^{O}P^{O}G$
lucidovarius Doe, 1937	$C^{W}B^{BY}SML^{B}P^{B}G$
luteus Simpson, 1920	$C^{W}B^{Y}SL^{O}P^{O}G$
margaretae Jones, 1979	$C^{W}B^{BY}SML^{B}P^{B}WG$
marmoratus Pilsbry, 1912	$C^{W}B^{BY}SML^{B}P^{B}G$, $C^{W}B^{BY}SE^{B}ML^{B}P^{B}G$
matecumbensis Pilsbry, 1912	$C^{W}B^{O}L^{Y}P^{O}G$, $C^{W}B^{Y}L^{Y}P^{O}G$
miamiensis Simpson, 1920	$C^{W}B^{BY}E^{BY}ML^{B}P^{B}AOG$, $C^{W}B^{BY}E^{BY}ML^{O}P^{O}AOG$
mosieri Simpson, 1920	$C^{Y}B^{O}L^{O}P^{O}G$
nebulosus Doe, 1937	$C^{W}B^{BY}SML^{B}P^{B}G$
ornatus Simpson, 1920	$C^{Y}B^{Y}L^{Y}P^{Y}AOG$, $C^{Y}B^{Y}L^{Y}P^{Y}AG$
osmenti Clench, 1942	$C^{W}B^{B}E^{B}ML^{B}P^{B}AOW$
pictus (Reeve, 1842)	$C^{W}B^{BY}SE^{BY}ML^{B}P^{B}AOW$
pseudopictus Simpson, 1920	$C^{W}B^{BY}SE^{B}ML^{B}P^{B}WG$
roseatus Pilsbry, 1912	$C^{W}B^{Y}L^{P}P^{P}AOG$, $C^{W}B^{Y}L^{Y}P^{Y}AOG$, $C^{W}B^{O}L^{O}P^{O}AOG$, $C^{W}B^{Y}L^{Y}P^{Y}G$
septentrionalis Pilsbry, 1912	$C^{W}B^{O}L^{O}P^{O}G$
simpsoni Pilsbry, 1921	$C^{W}B^{Y}L^{O}P^{O}AOG$, $C^{W}B^{Y}SL^{O}P^{O}AOG$
solidulus Pilsbry, 1912	$C^{W}B^{Y}SE^{Y}L^{O}P^{O}$
solidus (Say, 1825)	$C^{W}B^{Y}L^{O}P^{O}$
solisocassus De Boe, 1933	$C^{W}B^{BY}SE^{B}ML^{B}P^{B}AOG$, $C^{W}B^{BY}SE^{B}ML^{B}P^{B}AOWG$
splendidus Frampton, 1932	$C^{W}B^{BY}SML^{B}P^{B}G$
subcrenatus Pilsbry, 1912	$C^{W}B^{O}L^{O}P^{O}G$, $C^{W}B^{O}L^{Y}P^{O}G$
testudineus Pilsbry, 1912	$C^{Y}B^{B}SML^{B}P^{B}AOG$, $C^{Y}B^{B}SE^{B}ML^{B}P^{B}AOG$, $C^{Y}B^{B}SML^{B}P^{B}AG$, $C^{Y}B^{B}SE^{B}ML^{B}P^{B}AG$, $C^{Y}B^{B}SML^{B}P^{B}G$
vacaensis Simpson, 1920	$C^{W}B^{O}L^{O}P^{O}G$, $C^{W}B^{O}L^{Y}P^{O}G$
versicolor Simpson, 1920	$C^{Y}B^{B}SE^{B}ML^{B}P^{B}AO$, $C^{Y}B^{B}SML^{B}P^{B}AOW$
violafumosus Doe, 1937	$C^{E}B^{BY}SE^{B}ML^{B}P^{B}WG$
vonpaulseni Young, 1960	$C^{W}B^{BY}E^{B}ML^{B}P^{B}AOWG$
walkeri Clench, 1933	$C^{W}B^{BY}E^{B}ML^{B}P^{B}AOG$, $C^{W}B^{BY}E^{B}ML^{B}P^{O}AOWG$
wintei Humes, 1954	$C^{Y}B^{B}SE^{B}ML^{B}P^{B}AG$



Figs. 1–7. Body whorls of *Liguus fasciatus* showing representative color and banding elements. **Fig. 1.** *Dryas* bands (B). **Fig. 2.** Spreading of *dryas* band pigment. **Fig. 3.** Spreading of *dryas* band pigment and longitudinal marbling. **Fig. 4.** Vacant center of *dryas* bands and longitudinal marbling. **Fig. 5.** "Negative-*dryas*" pattern. **Fig. 6.** *Dryas* bands (B), sutural line (L), and peripheral line (P). **Fig. 7.** Punctate banding.

Presence of a narrow spiral line just below the suture is designated by L, a similar line at the periphery by P (Fig. 6). Pink coloring of the apex is designated by A, a pink columellar callus by O. A whitish suffusion (W) occurs all over the surface in some specimens, rendering the brown coloration bluish, purplish, or smoky gray.

A variable number of green spiral lines occurs in the periostracum (G). Their number, thickness, placement, and relation to the pattern in the underlying calcareous part of the shell seem to compose a complex system. The material we have examined does not permit a more detailed analysis at this time.

DISCUSSION

The 12 color and banding parameters defined above do not exhaust the variability shown by the *Liguus fasciatus* shell, but in their various combinations they account for all major morphotypes in the material examined by us. In Table 2 the notation is applied to the named infraspecific taxa of *L. fasciatus* in Florida. The general geographic distribution of character-states is shown on small-scale maps (Fig. 8). Two other maps (Figs. 9, 10) indicate the diversity of character-states present in each region.

The ability of this particular study to resolve the deployment of character-states is limited by the nature of the material (non-quantitative, presence-absence data; museum lots sorted to preconceived limits) and the regional scale of the analysis.

Nevertheless, it is apparent that most character-states are widely deployed throughout the Floridian range of *L. fasciatus*. There are no strictly allopatric alternative states. Yellow ground color, for instance, is less widespread than white, but at most localities both are present. Shells without *dryas* bands (B^0) occur farther north along the east coast than banded shells, but over most of the range both banded and unbanded are present. Brown (B^B) and yellow (B^Y) *dryas* banding co-occur extensively except at the western end of the mainland range.

Distribution of a character-state represents a minimum estimate of the distribution of its determinant allele. Bandless shells will not show band modifications such as mottling (M) or vacant centers (E), even if the relevant alleles are present in the genotype; the whitish suffusion (W) that produces light tones on a dark colored shell may not be detectable against a plain white ground.

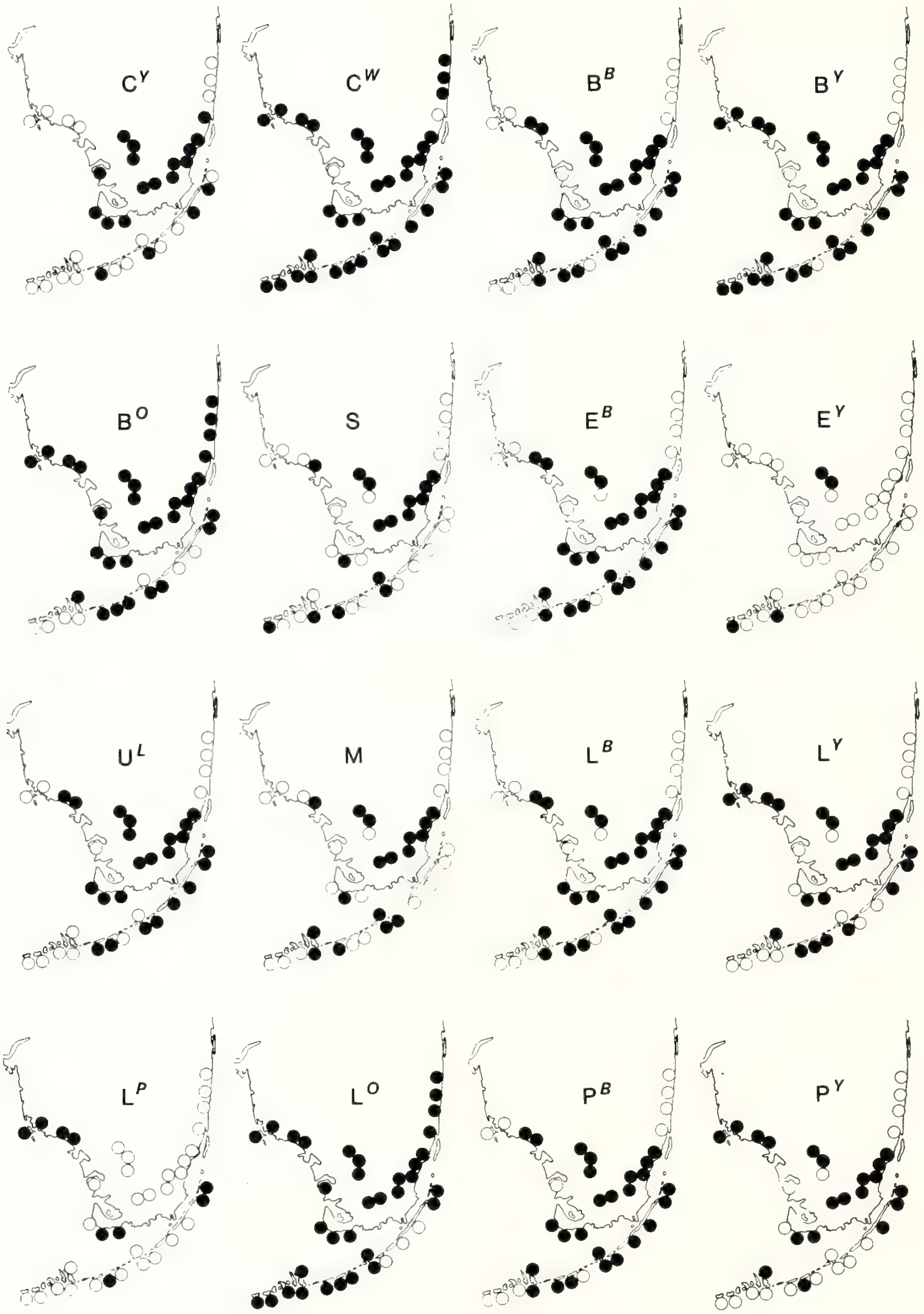


Fig. 8. Geographic distribution of character-states in southern Florida. C^{Y}, yellow ground color; C^{W}, white ground color; B^{B}, brown *dryas* bands; B^{Y}, yellow *dryas* bands; B^{O}, *dryas* bands absent; S, spreading of *dryas* band pigment; E^{B}, center of brown *dryas* band vacant; E^{Y}, center of yellow *dryas* band vacant; U^{L}, lower *dryas* band absent; M, marbling of *dryas* bands; L^{B}, brown sutural line; L^{Y}, yellow sutural line; L^{P}, pink sutural line; L^{O}, sutural line absent; P^{B}, brown peripheral line; P^{Y}, yellow peripheral line. P^{P}, pink peripheral line; P^{O}, peripheral line absent; A, pink apex; O, pink columella; W, white suffusion; G, periostracal green lines.

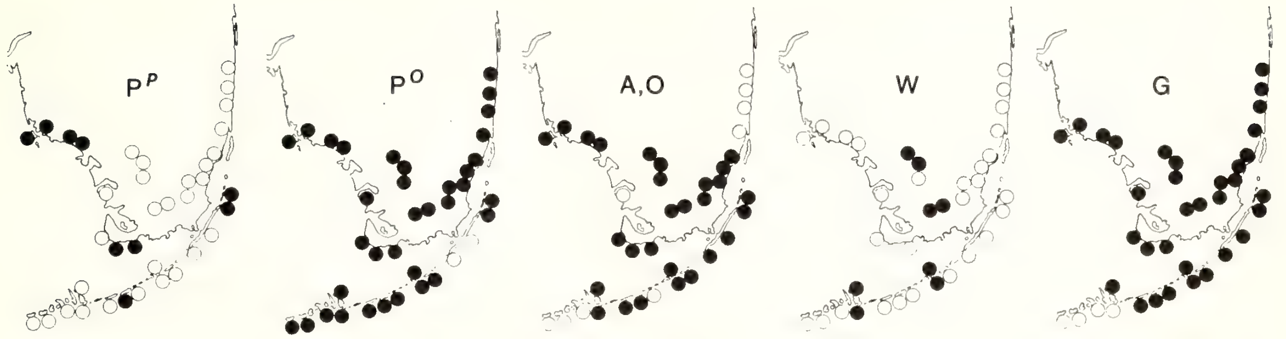
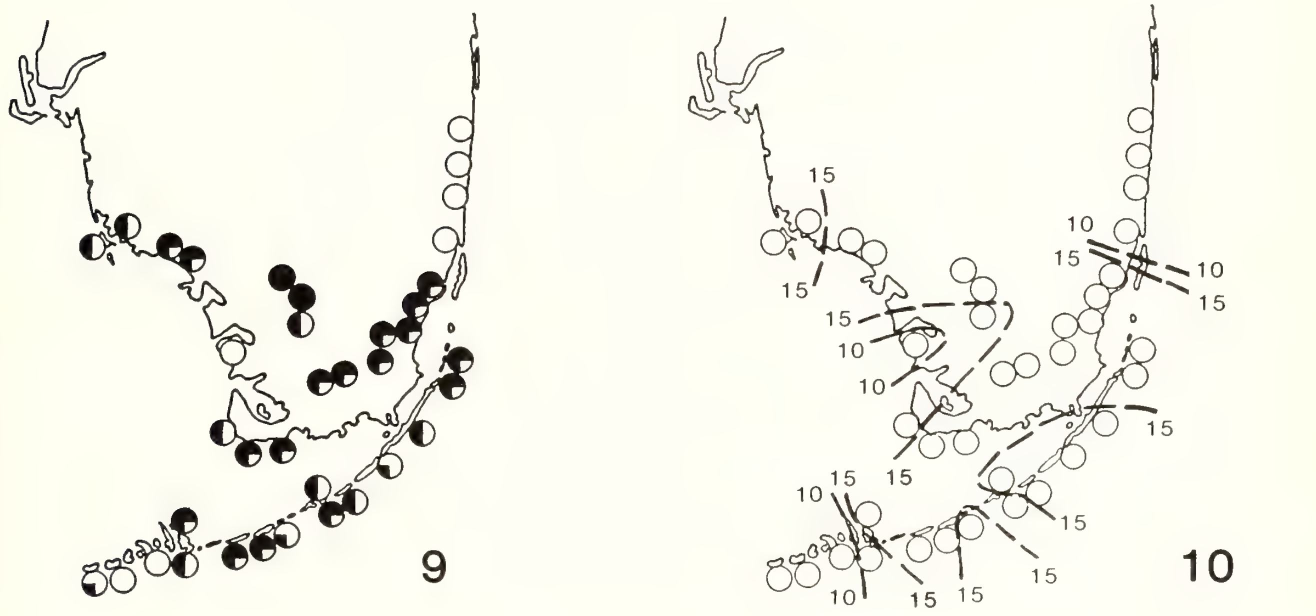


Fig. 8. continued.



Figs. 9–10. Character-state diversity in southern Florida. **Fig. 9.** Filling of circles indicates number of character-states present: open circles, 1–5; one-quarter filled, 6–10; half filled, 11–15; three-quarters filled, 16–20; solid circles, 21+. **Fig. 10.** Diversity contoured: dashed lines drawn at interpolated positions of 10 and 15 character-states, respectively.

On a regional scale, character-state diversity shows few obvious trends (Figs. 9, 10). The highest diversity is clustered in the Pinecrest area and on the Atlantic coastal ridge, but also in places along the upper and middle Keys and sporadically on the south and west coasts of the peninsula. The lowest diversity occurs along the east coast from Fort Lauderdale north and on the west coast in the vicinity of Lossman's Key. Low readings also occur on the Keys (interspersed with higher-diversity sites) and at the west end of the mainland range. Rather than a smooth diversity gradient in any direction, the basic array consists of a high-diversity core with intrusions from several directions by sectors of low diversity.

As a basis for further examination of *Liguus* evolution and biogeography, we propose the model of an originally widespread and genetically diverse population of *Liguus fasciatus*, subsequently fragmented and differentially culled by selection, in contrast to the notion of random dispersal *via* hurricane. Hurricane dispersal is a narrative explanation (*sensu* Ball, 1976)—essentially a story made up to fit the observed facts of distribution. Tuskes (1981) examined critically the likelihood of hurricane dispersal of *Liguus* over water. He noted that the snails do seal tenaciously to trees during winter, but that the hurricane season is during summer and fall while the snails are generally active and not in hibernation. Also, the mucus seal softens and opens up when moistened for extended periods. He found that, of the tree species inhabited by *Liguus*, ironwood and lignumvitae sink in sea water, and gumbo-limbo, dogwood, and poisonwood barely remain afloat in calm water; thus, many species of hammock trees are doubtfully suitable as rafts for *Liguus*, In two experiments, none of 30 snails on dogwood branches remained attached for more than a minute after the branches were placed in sea water. Snails placed on a board which was floated for two hours never came in contact with water more than 3 mm deep and were usually out of the water but moist; no individuals exposed to these conditions were alive 36 hours later (Tuskes, 1981). Tuskes concluded that active or inactive snails have an exceedingly low probability of surviving a 130 km trip in a hurricane to reach Florida from Cuba. Yet even this experimental evidence does not prove that certain *Liguus* were not dispersed by hurricane at some past time; it only suggests that the trip is a hard one. One cannot really falsify the hurricane explanation, but only ask whether external evidence supports random introduction as a major determinant of morph diversity and distribution, over development in situ of observed population characteristics.

Rex's (1972) study, in which hammock area was shown to be a good predictor and isolation a poor predictor of color morph diversity supports the model proposed here. If isolation translates into relative difficulty and rarity of a vagrant snail's reaching an insular hammock, the most remote hammocks should have had consistently fewer color morphs. Instead, it is the smaller hammocks, those with lower habitat diversity and less available habitat, which have lower morph diversity.

The regional trend shown in our study could equally well represent the effects of migration from a central core area, or the availability or quality of habitat. The trend does not support a distance-related gradient, similar to a "peninsular effect," based on migration from a Cuban source area.

The natural distribution of hammock vegetation is controlled in part by topography and drainage (Davis, 1943), with a few feet of elevation meaning the difference between hardwood forest (on higher ground) and mangrove, sawgrass marsh, or wet prairie (on lower ground). At past times of lowered sea level—as low as -60 m during the late Wisconsinan regression 17,000 yr B. P. (Blackwelder, Pilkey, and Howard, 1979)—the water table would also have been drawn down (Delcourt and Delcourt, 1981), possibly permitting many hammock areas that are now effectively islands to fuse in a much more extensive zone of hardwood forest. In addition, a substantially larger area of the Floridian Plateau would have been exposed above sea level (cf. Parker and Cooke, 1944, pl. 1). A pollen record from Lake Annie, central peninsular Florida, indicates a very dry climate from 37,000 to 13,010 yr B.P. with extensive *Ceratiola* (rosemary) sand dune scrub (Watts, 1975, 1980). Dry conditions, probably cooler than the present, would not be favorable for subtropical hardwood forest. However, the Lake Annie site, being in an area of dunes with distinctive endemic vegetation may be strongly influenced by local factors (Watts, 1980); in any case it is not likely to be representative of coastal and subcoastal situations. Delcourt and Delcourt (1981) placed the establishment of subtropical hardwood forest in southernmost Florida at about 5,000 yr B.P., but the only sampling site in this immediate area (Core 59T6) contains no pollen record older than this. Earlier data from the southern peninsula or the flooded part of the Floridian Plateau are lacking at present.

During still earlier transgressions of the sea inland, fragmentation of the forest must have been at least as extreme as that observed in historic times. Therefore a working historical model of potential *Liguus* habitat entails expansion alternating with shrinkage and fragmentation, correlated with the sea-level curve through time. As subaerial features, the upper Florida Keys are younger than 95,000 years old, the age obtained by uranium-series dating of reef coral of the Key Largo Limestone (Broecker and Thurber, 1965; Hoffmeister and Multer, 1968). This age gives a time-frame for the development of *L. fasciatus* populations and morph frequencies on these coral islands, although colonization must have taken place from source-populations already structured by selective pressures. Much of the mainland territory inhabited by *L. fasciatus* is underlain by Pleistocene marine formations judged penecontemporaneous with the Key Largo Limestone (Parker and Cooke, 1944). The lower Keys, composed of Miami Oolite, may have been emergent earlier (Christman, 1980) and might have served as refugia during times of high sea level.

The origin of *Liguus* as a genus and its occurrence in the general Antillean-south Floridian region probably extends much farther back in time. According to Clench (1967) *Liguus* is not closely related to any genera of Bulimulidae now existing in Central or South America. *Corona* Albers, 1850, of northern South America may be the nearest relative, but as Clench noted, the gap between the two genera is large in shell morphology, size, and type of coloration. High-spired, conical, spirally banded bulimulid snails with morphology suggesting an arboreal mode of life occur in the Eocene and Oligocene of the western interior of North America (McKenna, Robinson, and Taylor, 1962; Taylor, 1975) in a paleoenvironmental context of subtropical climate and ample rainfall. Some of the other land snail genera present there as fossils—*Caracolus* (Bishop, 1979) (Camaenidae); *Hemitrochus* (Taylor, 1975) (Helminthoglyptidae)—are now limited to the Antillean region. Their ranges evidently were restricted southward along with other tropical biota as the planetary temperature gradient steepened through the Tertiary Period and tropical conditions became limited to lower latitudes (Wolfe, 1978). Considered in this way, the distribution of modern *Liguus* may reflect a more general phenomenon—the equatorward restriction of the tropical American biota. This interpretation is supported by the many parallel instances of organisms with a similar history and indirectly by independent climatic evidence including oxygen isotope data (Savin, 1977; Wolfe, 1978).

A possible North American origin for the genus *Liguus* in the early Tertiary eliminates some of the conceptual problems of the hurricane mode of dispersal. There is a much longer time-frame available—tens of millions versus thousands of years—for the events placing ancestral members of the genus on the islands of Cuba and Hispaniola. At the species level, a test of the biogeography awaits a phylogenetic analysis of relationships within the genus; if *L. fasciatus* is found to be the bearer of derived rather than primitive characters with respect to the rest of the genus, then its present occurrence in Florida will have to be seen as young relative to the remainder of the group. At the infraspecific level, use of the shell color and banding parameters defined here will aid the search for pattern in, and processes acting upon, the elaborate polymorphism of *L. fasciatus*.

ACKNOWLEDGMENTS

For valuable discussion of *Liguus* and snail geography in general, we are grateful to Carl C. Christensen, Jane E. Deisler, and Paul M. Tuskes, while not necessarily claiming them as partisans of our views. We thank Professor A. J. Cain, Carl Christensen, Jane Deisler, and the Systematics Discussion Group of the California Academy of Sciences for critical comments on the manuscript and Archie L. Jones for an introduction to *Liguus* in the field.

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COMPARATIVE ANATOMY OF FOUR PRIMITIVE MURICACEAN GASTROPODS: IMPLICATIONS FOR TROPHONINE PHYLOGENY

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ABSTRACT

The main features of the shell, head-foot, pallial complex, alimentary and reproductive systems of *Trophon geversianus* (Pallas), *Boreotrophon aculeatus* (Watson), *Paziella pazi* (Crosse), and *Nucella lamellosa* (Gmelin) are described, and phenetic and cladistic analyses based on subsets of these data presented. Similarities in shell morphology revealed by phenetic studies are interpreted as being due to convergence, and are indicative of similar habitats rather than of close phylogenetic relationships. Convergences are also noted in radular and stomach characters. Cladistic analyses of anatomical data support the following conclusions: 1) Thaididae are a primitive and ancient family of muricaceans forming a clade equal in taxonomic rank with Muricidae; 2) Within Muricidae, *P. pazi* more closely resembles the ancestral muricid phenotype than any trophonine; 3) Trophoninae comprise a comparatively recent monophyletic group with differences due to a subsequent austral adaptive radiation.

The Muricidae are considered to be the most primitive family within Neogastropoda according to most (Thiele, 1929; Wenz, 1941; Taylor and Sohl, 1962; Boss, 1982) but not all (Golikov and Starobogatov, 1975) recent classifications. Of the five subfamilies of Muricidae, the Trophoninae, proposed by Cossmann (1903) on the basis of shell and opercular characters to include a number of boreal and austral species, are the most poorly understood. The systematic status and affinities of the Trophoninae have been the subjects of varying interpretations. Ponder (1973) considered this group to be the most primitive subfamily of the Muricidae, while Vokes (1971) suggested that at least some trophonines are descended from an early muricine lineage. Cossmann (1903) and Bouvier (1888) both considered Trophoninae to be intermediate between Muricinae and Thaididae.

In the most recent systematic revision of the Muricidae, Radwin and D'Attilio (1976:13) consider the Trophoninae "a subfamilial category for the sake of convenience," and note (1976:2) that "within the Trophoninae, relationships and even species delimitations are so poorly understood, . . . , that we have attempted nothing beyond describing and illustrating the type species of the more plausible genera". These authors (1976) transferred several genera (eg. *Austrotrophon* Dall, 1902; *Zaccatrophon* Hertlein and Strong, 1951) from the Trophoninae to the Thaididae on the basis of radular characters, and appear to support the hypothesis that Trophoninae are polyphyletic, citing (Radwin and D'Attilio, 1976:13) a personal communication from E. H. Vokes "it appears likely that the most northern trophons are derived from the *Paziella-Poirieria* line, and that the several austral forms that are unquestionably "trophonine" are probably derived from the Thaididae".

Thus, according to most published work, the Trophoninae are in a position to shed light on the systematics and the primitive morphology of the Muricacea. Taxonomic works on this group have been few, and these limited to studies of the morphologies of the shell, operculum and, in some cases, radulae (Strebel, 1904; Powell, 1951; Ponder, 1972; Houart, 1981).

What little is known of trophonine anatomy is limited to portions of the alimentary, reproductive and nervous systems of a handful of species (Bouvier, 1888; Eales, 1923; Taki, 1938; Smith, 1967; Houston, 1976). In contrast, the spawn and/or early development of over a dozen species have been studied (Jeffreys, 1867, Melvill and Standen, 1898; Strebel, 1904; Hedley, 1917; Lamy, 1928; Lebour, 1936; Thorson, 1940, 1946; Fioroni, 1966; Zaixso, 1973; Penchaszadeh, 1976; Picken, 1979).

The present study has as its objectives to present accounts of the anatomy and shell morphology of: 1) *Trophon geversianus* (Pallas, 1774), the type species of the type genus of Trophoninae, and an example of an intertidal austral species, 2) *Boreotrophon aculeatus* (Watson, 1882), an example of a bathyal "northern trophon", 3) *Paziella pazi* (Crosse, 1869) a primitive muricine from a line hypothesized

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to be ancestral to Trophoninae, and 4) *Nucella lamellosa* (Gmelin, 1791) an intertidal boreal example of the Thaididae, and on the basis of these data, to investigate the phylogenetic relationships between these taxa using phenetic and cladistic techniques.

MATERIALS AND METHODS

The following preserved material was used in this study:

Trophon geversianus 3 ♂ and 2 ♀ Intertidal rocks, Puerto Basil Hall, Isla de los Estados, Tierra del Fuego, Argentina (54°45.45'S,64°10.1'W) USARP-SOSC-R/V HERO (LACM 71-289) 2 ♂ and 1♀ Puerto Madryn, Argentina (USNM 841239) 2 ♀ Punta Arenas, Chile (ANSP A9442)

Boreotrophon aculeatus 7 ♂ and 4 ♀ COLUMBUS ISELIN sta. CI-161, Tongue of the Ocean, Bahamas (23°40'N,77°06'W) in 1370 meters. (voucher specimens USNM 841240)

Paziella pazi 1 ♂ and 1 ♀ PILLSBURY sta. P-984, W. of Anguilla, Leeward Islands (18°26.4'N, 63°12.6'W) in 421–439 meters. (voucher specimen USNM 841241)

Nucella lamellosa 4 ♂ and 2 ♀ Intertidal rocks, Deception Pass, Fidalgo Island, Puget Sound, Washington (USNM 841242)

Dry material from the USNM collections was used to supplement shell measurement data.

Specimens for anatomical studies were immersed in 10% hydrochloric acid (HCl) until the shells dissolved. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection. Dry shells were cracked in a vise in order to examine internal surfaces. Scanning electron micrographs were taken using a Cambridge 100 SEM. Phenetic analyses were conducted using mean values of the 13 continuous variables listed in table 1. Characters include eight morphometric descriptors of generalized shell shape (Harasewych, 1982) and five morphometric and sculptural parameters. The CLUSTAN cluster analysis program (Wishart, 1978) was used to standardize the data so that each character had a mean of zero and a standard deviation of one, to produce a matrix of inter-taxa distances using squared Euclidian distance, and to generate phenograms using both unweighted pair-group arithmetic averaging (UPGMA) and Ward's method (error sum of squares) clustering algorithms.

Table 1. Shell characters used in phenetic analyses of relationships between muricacean taxa. Characters 1 through 8 describe geometry of the generalized shell form (Harasewych, 1982).

1. Shape of the generating curve of the body cavity (Sbc)
2. Shape of the generating curve of the siphonal canal (Ssc)
3. Relative siphonal length (Rsl)
4. Siphonal angle (beta)
5. Rate of whorl expansion (W)
6. Angle of the generating curve (theta)
7. Position of the generating curve relative to the axis (D)
8. Rate of whorl translation (T)
9. shell length (L)
10. shell width/shell length (W/L)
11. aperture length/shell length (AL/L)
12. Number of whorls of teleoconch (# whorls)
13. Number of varices/lamellae on the final whorl (# var)

Cladistic analysis is based on 15 qualitative anatomical characters. Character polarizations are based on the criterion of outgroup comparison. Discussion of the choice of outgroups requires a review of the taxonomy of rachiglossan gastropods. The majority of the literature (as exemplified by Taylor and Sohl, 1962) divides the suborder Rachiglossa into three superfamilies: Muricacea, Buccinacea and Volutacea. Ponder (1973) includes all rachiglossan gastropods in one superfamily, the Muricacea, recognizing 17 families as "more-or-less equally distinct." The present paper uses the earlier classification, recognizing Muricacea, Buccinacea and Volutacea as subgroups of Rachiglossa, although not strongly advocating superfamily status for each group. Muricacea is used in the sense of Radwin and D'Attilio (1971) with the exception that Columbariidae has been transferred to Volutacea (Harasewych, 1983). As it is unclear whether Buccinacea or Volutacea is more closely related to Muricacea, and as neither group has all the characters used in this study, both are used for outgroup comparison. The tendency toward parallelism in the evolution of the major organ systems within Rachiglossa has been well documented (Ponder, 1973). In several cases both primitive and presumably convergently derived characters are present in some outgroups. In such instances the character states of the most primitive members of the outgroups, as determined from existing taxonomic works, were considered to be primitive. The Wagner 78 program (Farris, 1970; Wiley, 1981) was used to generate a Wagner Tree of the 4 taxa. The Largest Clique Program, version 2.0 of Felsenstein was used to analyze compatibility of the anatomical characters. Results of these analyses are then compared with ecological data and with evidence from the fossil record, and a most parsimonious phylogenetic classification is proposed.

Some of the data used for character polarizations are based on unpublished observations and are identified by the writer's initials following such information.

The repositories of figured and examined specimens are indicated by the following abbreviations:

ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum (Natural History)
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology
USNM	National Museum of Natural History, Smithsonian Institution

RESULTS

MORPHOLOGY

Trophon geversianus (Pallas, 1774)
(Figs. 1–3, 15, 19–25)

This is the type species of the genus *Trophon* Montfort, 1810 (as *Murex magellanicus* Gmelin, 1791) by original designation. The fate of the subfamilial name Trophoninae, therefore, is dependent on the systematic position of this species. *Trophon geversianus* is common intertidally and subtidally in the Magellanic region. Shell morphology is very variable, the numerous morphs having been amply figured by Strebel (1904), who also included and extensive synonymy.

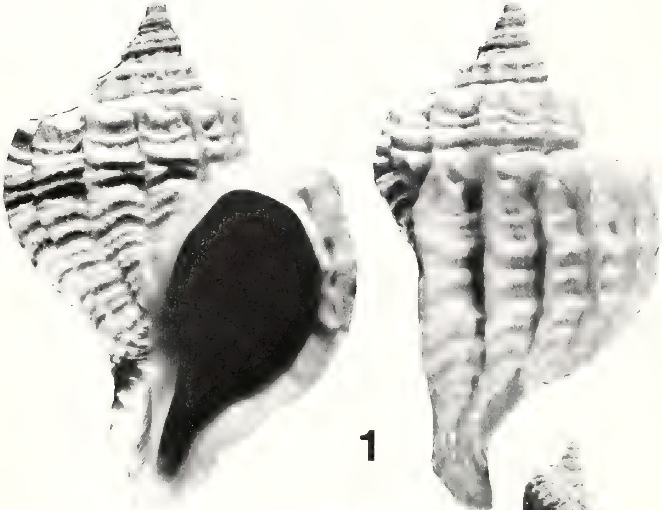
Shell morphology: Shell large (to 90 mm), moderately thin, globosely fusiforn (Figs. 1,2). Protoconch (Fig. 15) of 1¼ whorls, inflated, glassy, pitted. Transition to teleoconch abrupt, marked by appearance of spiral and axial sculpture. Teleoconch with up to 6 inflated whorls. Spire angle 58–91°. Axial sculpture of 16–21 lamellae per whorl. These may be flaring (Fig. 1) or smooth and barely perceptible (Fig. 2), especially in young or eroded specimens. Spiral sculpture of 12–20 cords on the last whorl and 4–6 on the penultimate whorl, with 0–1 fine threads between. Suture abutted, shoulder rounded to tabulate. Aperture broadly elliptical, deflected from coiling axis by 15–20°. Siphonal canal about ½ as long as the aperture, open, axial or only slightly deflected, in which case a pseudo-umbilicus is present. Inner lip smooth, appressed. Outer lip smooth, flaring. Shell color ranges from white to dark brown. Aperture reddish brown with a lighter marginal band. Fractured shells reveal smooth, topographically simple internal surfaces. Operculum (Fig. 3) broadly unguiculate, with nucleus terminal in juveniles and subterminal in larger specimens. Attachment area elliptical, internal surface thickened and unattached along abaxial and anterior margins. Anterior area abraded or broken in most specimens.

Animal—external features: The body consists of roughly 2½ whorls, of which the mantle cavity spans 2⁄3 whorl, the kidney 1⁄3 whorl and the digestive gland-gonad about 1¼ whorl. The columellar muscle is large and has a broad attachment area. Preserved animals are uniformly tan in color. The mantle edge is smooth, the siphon (Fig. 19,s) short. Tentacles are short and blunt, with large black eyes. The foot is broad and rectangular, with a glandular sole and a prominent propodial groove (Fig. 20,pg). An accesory boring organ (Fig. 20,abo) is situated medially, just behind the propodial groove.

Pallial complex: The mantle cavity is broad and high, with pallial organs arranged as in other rachiglossans. The osphradium (Fig. 19,os) is short, wide (L/W = 2) and asymmetrical, with 40–45 broad leaflets above and 30–35 narrow leaflets below the thick osphradial ganglion. The adjacent ctenidum (Fig. 19,ct) is twice as wide and twice as long as the osphradium, and contains 200–240 triangular leaflets. To its right lies the thick, purplish hypobranchial gland (Fig. 19,hg), and to its right, the rectum (Fig. 19,r) and genital ducts, which are enclosed in connective tissue and occupy a considerable volume, thereby raising the ceiling of the mantle cavity. A large pericardium (Fig. 19,pc) borders the left rear wall of the mantle cavity. The kidney (Fig. 19,k) with a large nephridial gland (Fig. 19,ng) that overlies much of the pericardium, empties into the mantle cavity through its right rear wall (Fig. 19,ko).

Alimentary system: The pleurembolic proboscis is short and broad, and when retracted, the buccal musculature projects beyond its posterior limits and abutts against the gland of Leiblein. From the mouth (Fig. 21,m) situated at the tip of the proboscis, a short oral tube leads to the buccal cavity. The radular ribbon (Fig. 21,rs) is long (0.4 shell length, n = 5), extending beyond the rear of the buccal mass and containing 228–243 rows of teeth (n = 5). The rachidian (Fig. 25) is broad, five-cusped, with the central and outer cusps strong and blunt, and the intermediate cusps shorter and partially fused to the inner edges of the outer cusps. Lateral teeth have a single scythe-shaped cusp emanating from a short basal area. There is a modified medial jaw or "sclerite" (Carriker, 1943) on the dorsal edge of the buccal cavity anterior to the esophageal opening. The esophagus runs posteriorly with ducts of the salivary glands adherent but not embedded. At the rear of the buccal mass are two pairs of salivary glands: the golded, tubular accessory salivary glands (Fig.21,asg) are embedded in the normal salivary glands (Fig.21,sg). Posterior to the conical valve of Leiblein (Fig. 21, vl) the esophagus passes through the nerve ring (Fig. 21,nr), widens and loops dorsally (Fig. 21,hl) along the left anterior portion of the gland of Leiblein (Fig. 21,gl). It is joined by a duct from this gland before constricting and running posteriorly along the floor of the cephalic sinus. The posterior esophagus passes under the kidney and ascends the left side of the digestive gland (Fig. 19,dg) where it joins the simple, tubular stomach (Figs. 19,24,sto). A mid-dorsal incision reveals that both ducts to the digestive gland are near the esophageal opening, and that the posterior mixing area is greatly reduced. The intestine runs anteriorly, expanding slightly along the pallial gonoduct to form the rectum (Figs. 19,24r) and detaching several millimeters before forming the anus (Fig. 21,a). No trace of an anal gland was found in any of the specimens examined.

Female reproductive system: A large, acinous ovary lines the columellar side of the digestive gland along its entire length. From it, a thin-walled oviduct leads to the rear of the mantle cavity without giving rise to a gonopericardial duct. The pallial gonoduct consists of an albumen gland (Fig. 22, ag) that joins the rear of the capsule gland (Fig. 22,cg), which, when viewed in transverse section, can be seen to consist of left and right lobes each with dorsal and ventral glandular areas similar to those of *Nucella lapillus* (Fretter, 1941). A blind, muscular bursa copulatrix (Fig. 22,bc) joins the duct that leads from the female opening to the capsule gland. The ventral pedal gland is situated along the midline of the foot, just behind the accessory boring organ. Egg capsules (Fig. 23) are stalked, have a medial hatching aperture and contain 5–37 ova (Zaixso, 1973).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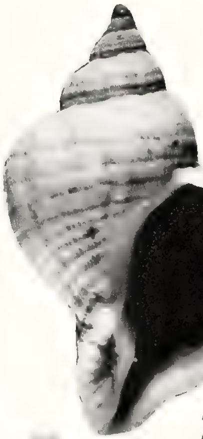
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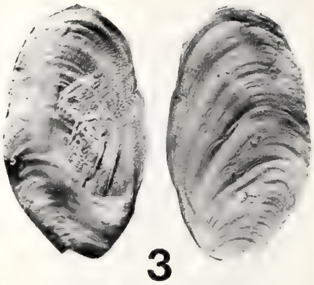
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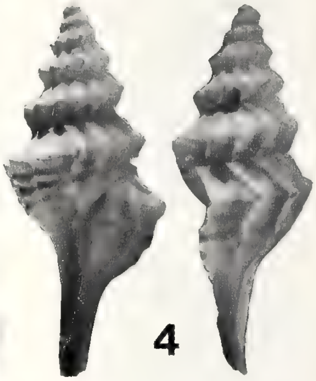
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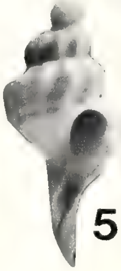
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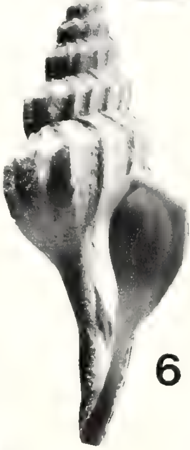
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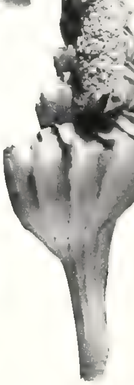
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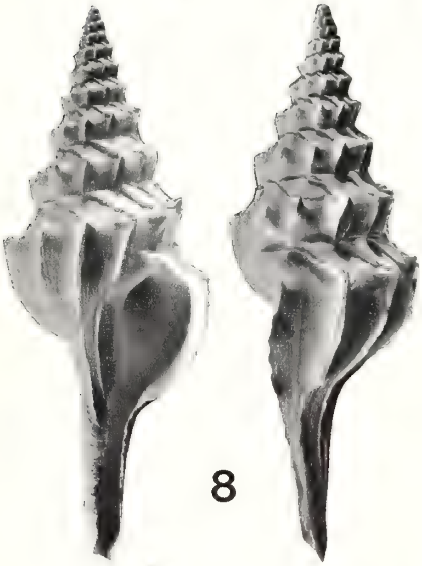
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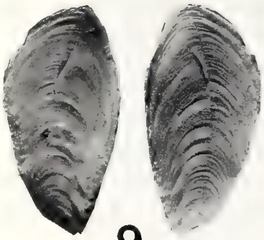
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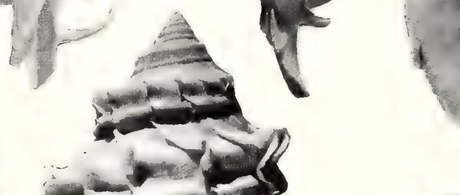
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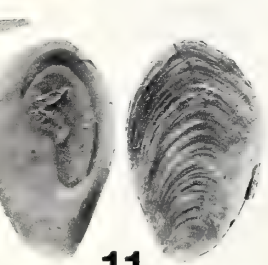
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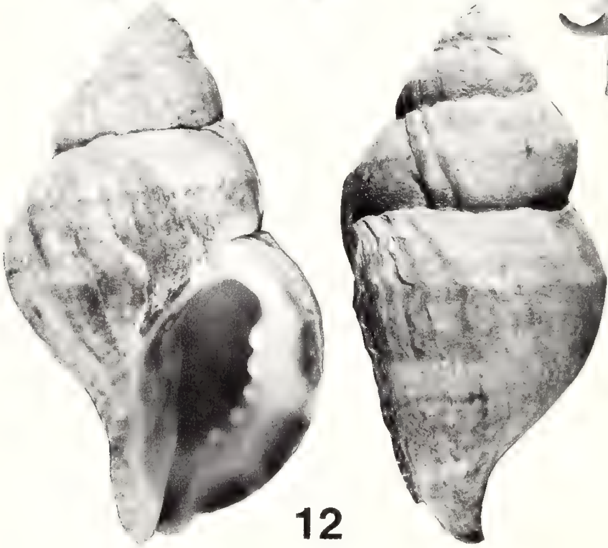
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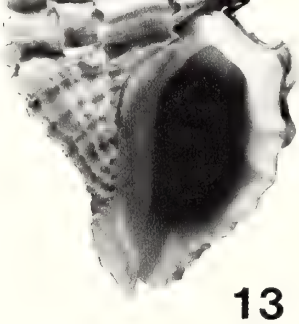
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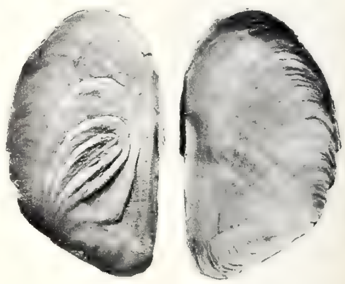
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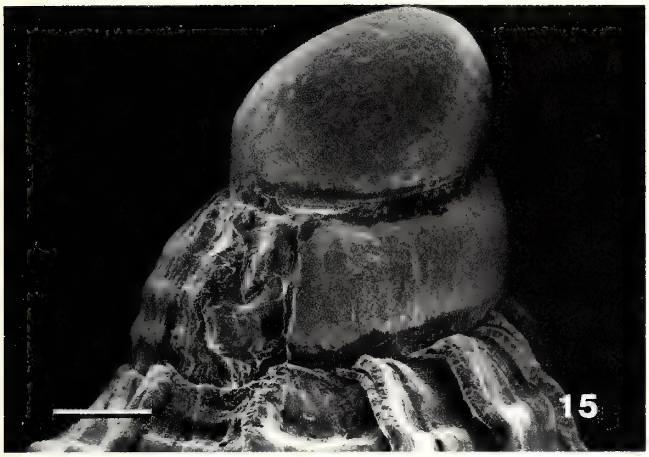

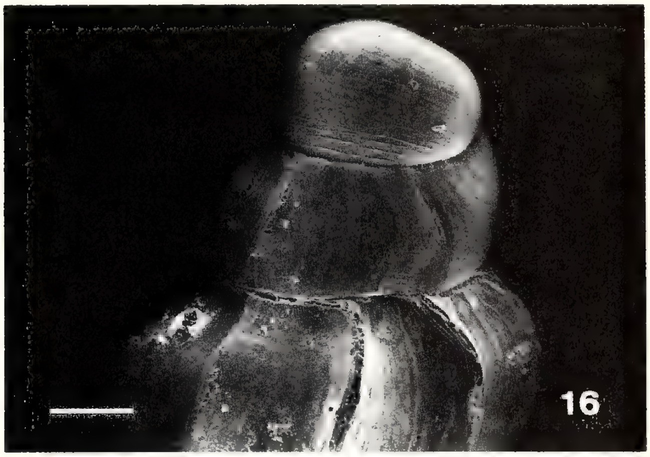

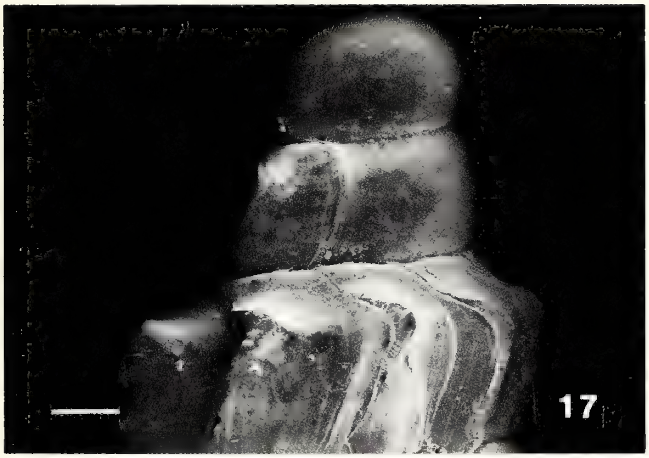

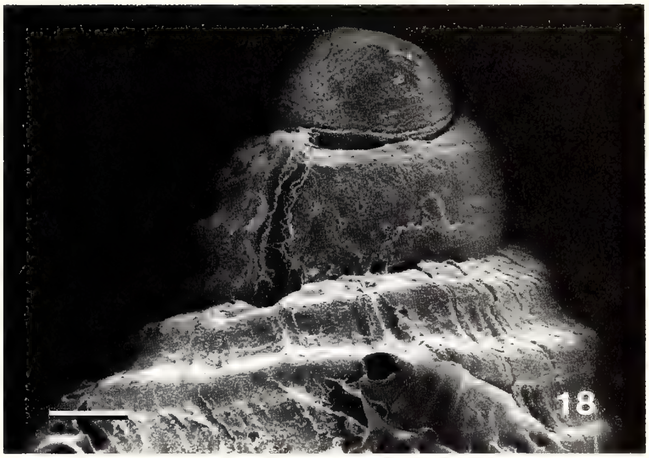

Figs. 15–18. Scanning electron micrographs of protoconchs. **15,** *Trophon geversianus*. Scale bar = 500 μm. **16,** *Boreotrophon aculeatus*. Scale bar = 250 μm. **17,** *Paziella pazi*. Scale bar = 250 μm. **18,** *Nucella lamellosa*. Scale bar = 250 μm.

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Figs. 1–3. *Trophon geversianus* (Pallas). **1,** Intertidal rocks, Puerto Basil Hall, Isla de los Estado, Tierra del Fuego, Argentina (54°45.45′S,64°10.1′W) USARP-SOSC-R/V HERO (LACM 71-289), Horizontal Width (HW) = 28.7 mm for apertural view, HW = 24.7 mm for lateral view. **2,** Puerto Madryn, Argentina (USNM 841239) HW = 22.0 mm. **3,** operculum of specimen in figure 2, HW = 7.2 mm.

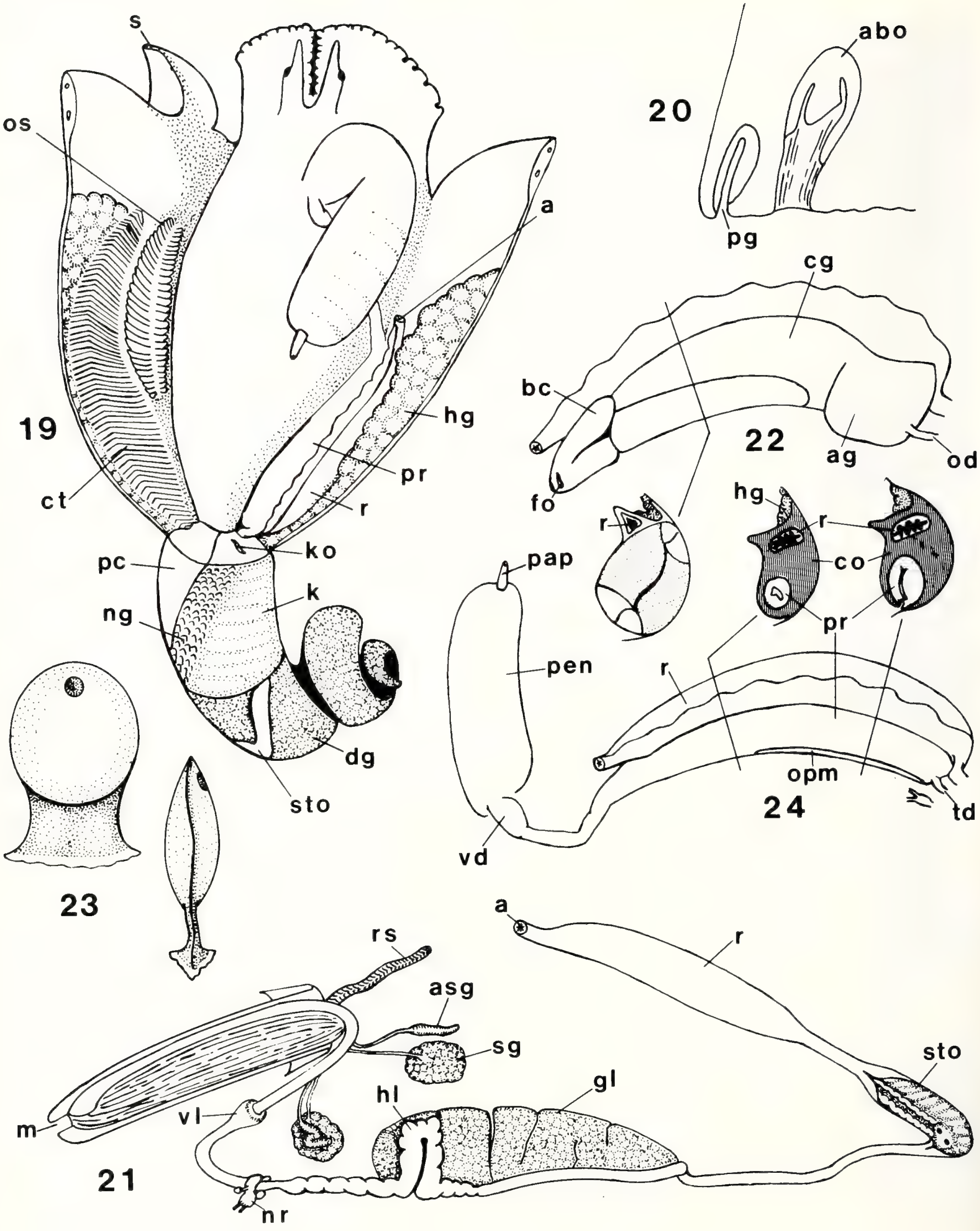
Figs. 4–5. Syntypes of *Trophon aculeatus* Watson. CHALLENGER sta.122, off Pernambuco, Brazil. (9°5′S,34°50′W) in 350 fathoms. [BM(NH) 1887.2.9.576-7] **Fig. 4** HW = 5.0 mm for apertural view, HW = 4.25 mm for lateral view. **Fig. 5** HW = 1.88 mm.

Fig. 6. Holotype of *Boreotrophon lacunellus* (Dall). BLAKE sta. 163, off Guadeloupe, in 769 fathoms. (MCZ 7312) HW = 14.7 mm.

Figs. 7–9. *Boreotrophon aculeatus* (Watson). COLUMBUS ISELIN sta. CI-161, Tongue of the Ocean, Bahamas (23°40′N, 77°06′W) in 1370 meters. (USNM 841240), **Fig. 7** HW = 10.0 mm **Fig. 8** HW = 12.0 mm for apertural view, 11.0 mm for lateral view **9,** operculum of specimen in figure 8 HW = 3.0 mm.

Figs. 10–11. *Paziella pazi* (Crosse). PILLSBURY sta. P-984, W of Anguilla, Leeward Islands (18°26.4′N,63°12.6′W) in 421–439 meters. (USNM 841241), **Fig. 10** HW = 18.0 mm including spines for apertural view only, HW = 16.0 mm including spines for lateral view, **Fig. 11** HW = 3.4 mm.

Figs. 12–14. *Nucella lamellosa* (Gmelin). **12,** intertidal rocks, Deception Pass, Fidalgo Island, Puget Sound, Washington. (USNM, 841242) HW = 26.0 mm for apertural view, HW = 22.0 mm for lateral view. **13,** Point Wells, Snohomish Co., Washington (48°40′N,122°24′W) SCUBA in 12.0 meters. (USNM 655925) HW = 37.0 mm **14,** operculum of specimen in figure 12 HW = 7.4 mm.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Male reproductive system: The ripe testis lines the columellar side of the visceral mass from its apex to just behind the kidney. It gives rise to a testicular duct (Fig. 24,td) that runs anteriorly, entering the mantle cavity just above the visceral ganglia and expanding to form the prostate gland (Fig. 24,pr). The prostate gland and rectum are joined by connective tissue (Fig. 24,co) to form a large cylindrical mass that runs half the length of the mantle cavity. The lumen of the prostate gland is in the form of a longitudinal slit, and communicates with the mantle cavity along the posterior ⅔ of its length (Fig. 24,opm). Below the anus, the testicular duct constricts, becomes muscular, and descends to the floor of the mantle cavity (Fig. 24,vd) expanding slightly before reaching the base of the penis. The broad, dorsoventrally compressed penis (Fig. 24,pen) extends half the length of the mantle cavity and has a terminal papilla (Fig. 24,pap).

Boreotrophon aculeatus (Watson, 1882)
(Figs. 4–9, 16, 26, 29–31)

This species was described on the basis of two very young specimens (4¾ and 2⅓ postnuclear whorls, Figs. 4,5) taken by the CHALLENGER Expedition in 640 meters off Pernambuco (now Recife), Brazil. Several years later, Dall (1889) proposed the taxon *Boreotrophon* (*aculeatus* Watson var.?) *lacunellus* based on a single large specimen (Fig. 6) from 1,406 meters off Guadeloupe. In his description, Dall stated "It is most closely related to *T. aculeatus* Watson, from deep water off Pernambuco, and I am disposed to consider them the same, . . .". Comparison of the type specimens of both nominal taxa with additional specimens, including juveniles referred to by Dall (1889) as "young specimens of what I suppose to be the same species," leaves little doubt that the taxon *B. lacunellus* Dall does not warrant even subspecific distinction from B. aculeatus (Watson).

This species inhabits sand and mud bottoms at depths ranging from 400 to 1,400 meters, and has been taken off North Carolina, the Bahamas, the Lesser Antilles and Brazil as well as in the Gulf of Mexico. The presence of polychaete tubes (Fig. 7) on several specimens indicates an epifaunal habitat.

Shell morphology: Shell small (to 40 mm), thin, narrowly fusiform (Figs. 4–8). Protoconch of 1¼ whorls, inflated, glassy, with 18–20 fine spiral threads on some (Fig. 16) but not all specimens. Transition to teleoconch distinct but not pronounced. Teleoconch with up to 10 sharply shouldered whorls. Spire angle 32–37°. Axial sculpture of 10–13 lamellae. Spiral sculpture generally absent, although young specimens may have 3–6 weak cords on the last whorl (Fig. 4). Suture adpressed. Aperture ovate, deflected from coiling axis by 10–15°. Siphonal canal slightly longer than aperture, open, axial. Inner lip smooth, appressed. Outer lip smooth, flaring. Shell and aperture color pure white. Internal surfaces are smooth and topographically simple. Operculum (Fig. 9) is narrowly unguiculate, terminally nucleate, with anterior and abaxial margins thickened. Nucleus often abraded or broken.

Animal—external features: The shell-less animal comprises 3 whorls, the mantle cavity overlying 1 whorl, the kidney occupying ¼ whorl and the digestive gland-gonad 1½ whorls. Preserved animals were retracted 2⁄3 whorl within the aperture, and were uniformly pale tan in color. The mantle edge is smooth, the siphon long, and tentacles short and broad. The foot is broad, short, squarish, with a deep propodial groove and a small medial accessory boring organ.

Pallial Complex: The mantle cavity is narrow, deep and low. The osphradium is very wide (L/W = 2) and extremely assymmetrical, with 52–57 broad leaflets above and 28–33 short leaflets below the osphradial ganglion. The ctenidium is slightly narrower than and over twice as long as the osphradium, and has 110–130 deeply hanging triangular leaflets. The hypobranchial gland is thick, purplish, transversely pleated. The rectum and genital ducts are surrounded by connective tissue, but are not nearly as large as in the preceding species. The pericardium is small, and is bordered on the right by a narrow nephridial gland and kidney.

Alimentary system: The proboscis is short, stout, pleurembolic. Large cartilages support the radular ribbon, which is 1.5 times as long as the buccal mass, but only 0.1 times the shell length. The radula (Fig. 26) consists of 109–138 rows of teeth (n = 5). Rachidia are broad and have wide, simple basal areas. The central and outer cusps are stout and heavily buttressed anteriorly, the intermediate cusps are shorter and sharper. Lateral teeth have a wide basal plate and a long scythe-shaped single cusp. A broad cartilaginous jaw is situated along the anterior dorsal edge of the buccal cavity. From the buccal mass, the esophagus runs posteriorly and expands into a wide valve of Leiblein (Fig. 29,vl). Ducts of the normal salivary glands become embedded in the esophagus just anterior to the valve of Leiblein, while ducts of the accessory salivary glands join ventral to the esophagus to form a single duct that runs anteriorly. The esophagus passes through the nerve ring (fig. 29,nr), runs posteriorly along the floor of the cephalic sinus, under the

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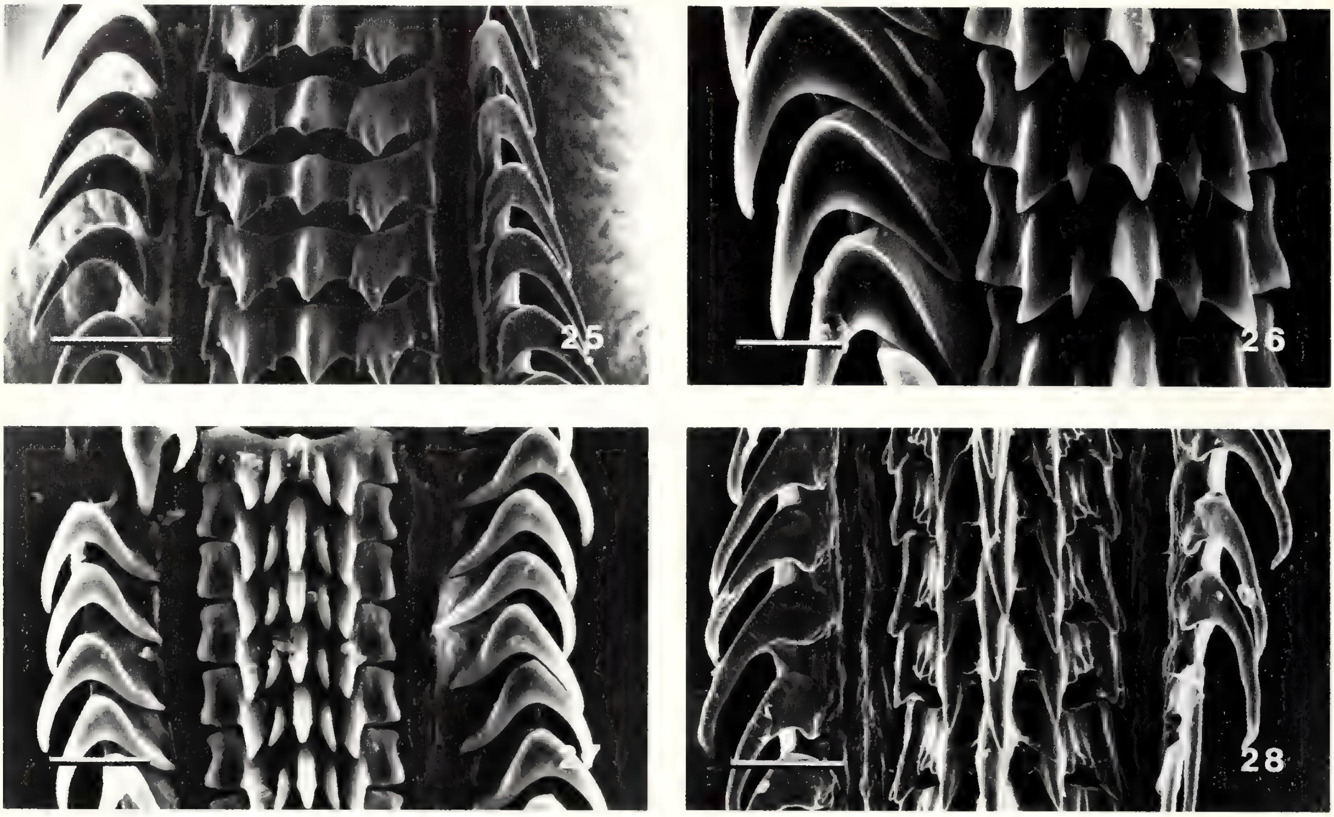
Figs. 19–24. *Trophon geversianus.* **19,** male specimen removed from its shell, partially uncoiled, with the mantle cavity opened mid-dorsally to display its contents. **20,** sagittal section through the anterior portion of the foot. **21,** Diagrammatic representation of the alimentary system. **22,** the female pallial gonoduct, including a transverse section through the capsule gland and rectum. **23,** anterior and lateral views of an egg capsule. **24,** the male pallial gonoduct, including two transverse sections through the prostate gland and rectum. a, anus; abo, accessory boring organ; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; co, connective tissue; ct, ctenidium; dg, digestive gland; fo, female opening; gl, gland of Leiblein; hg, hypobranchial gland; k, kidney; ko, kidney opening; m, mouth; ng, nephridial gland; nr, nerve ring; od, oviduct; opm, pallial opening of prostate; os, osphradium; pap, papilla; pc, pericardium; pen, penis; pg, propodial groove; pr, prostate gland; r, rectum; rs, radular sac; s, siphon; sg, salivary gland; sto, stomach; td, testicular duct; vd, vas deferens; vl, valve of Leiblein.



Figs. 25–28. Scanning electron micrographs of radulae. **25,** *Trophon geversianus.* Scale bar = 100 μm. **26,** *Boreotrophon aculeatus.* Scale bar = 20 μm. **27,** *Paziella pazi.* Scale bar = 25 μm. **28,** *Nucella lamellosa.* Scale bar = 100 μm.

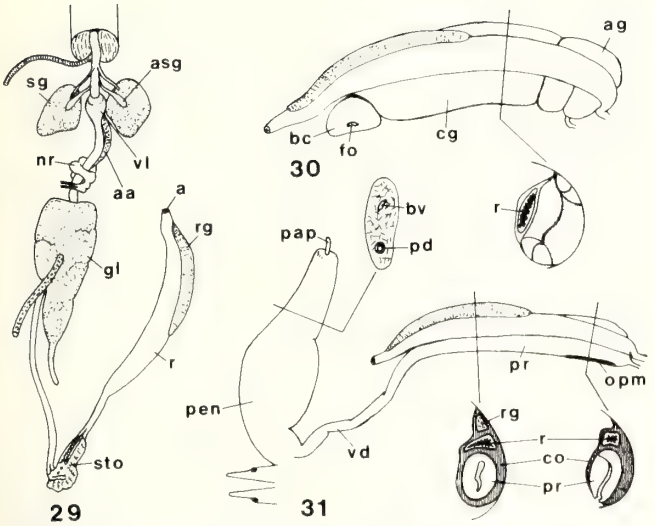
large dark brown gland of Leiblein (Fig. 29,gl), and is joined by a duct from this gland just behind its anterior edge. The anterior aorta (Fig. 29,aa), which paralleled the esophagus until this point now turns dorsally, ascends to the top of the gland of Leiblein, passing between adpressed folds of this highly convoluted gland, and descends along its left side before again running alongside the esophagus. The esophagus continues posteriorly to join the stomach, which differs from the preceding species in having a large posterior mixing area, but agrees in most respects with that of *Boreotrophon truncatus* (Ström, 1768) figured by Smith (1967, text-fig. 2, as *Trophon truncatus*). The intestine passes through the kidney and runs along the right wall of the mantle cavity before detaching and ending in an anus (Fig. 29,a). A large anal gland (Fig. 29,rg) runs dorsal to the rectum (Fig. 29,r) for half its length.

Female reproductive system: The ovary and upper oviduct do not differ from those of *T. geversianus*. The pallial oviduct, however, is proportionally narrower, and the crest along the rectum is reduced. The albumen gland (Fig. 30,ag) is narrower and more tubular, and its juncture with the capsule gland (Fig. 30,cg) is more constricted. The bursa copulatrix (Fig. 30,bc) consists of a simple, muscular tube the leads from the female opening (Fig. 30,fo) to the capsule gland without giving rise to a diverticulum. The ventral pedal gland is simple and shallow. Morphology of the egg capsules is unknown.

Male reproductive system: As in *T. geversianus*, a simple, tubular testicular duct leads from the testis to the rear of the mantle cavity. The prostate gland (Fig. 31,pr) opens into the mantle cavity through a short ventral slit (Fig. 31,opm). It is joined to the rectum by connective tissue (Fig. 31,co), but without forming the voluminous mass that occurs in *T, geversianus*. The vas deferens (Fig. 31,vd) descends to the floor of the mantle cavity just below the anus, and continues anteriorly to the the base of the penis, where it becomes expanded and very muscular. The penis (Fig. 31,pen) is broad and flattened, extends half the length of the mantle cavity, and has a pronounced terminal papilla (Fig. 31,pap).

Paziella pazi (Crosse, 1869)
(Figs. 10, 11, 17, 27, 32–34)

The genus *Paziella* dates back to the Upper Cretaceous, and is presently considered to be the oldest of muricine genera (Vokes, 1970). Similarities between *Paziella pazi*, the type species of the genus, and certain trophons have been noted by Dall (1889). More recently, Vokes (1971) has suggested that the Trophoninae, at least in part, are an



Figs. 29–31. *Boreotrophon aculeatus.* **29,** diagrammatic representation of the alimentary system. **30,** the female pallial gonoduct, including a transverse section through the capsule gland and rectum. **31,** the male pallial gonoduct, including two transverse sections through the prostate gland and one through the penis. a, anus; aa, anterior aorta; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; bv, blood vessel; cg, capsule gland; co, connective tissue; fo, female opening; gl, gland of Leiblein; nr, nerve ring; opm, pallial opening of the prostate; pap, papilla; pd, penial duct; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; sg, salivary gland; sto, stomach; vd, vas deferens; vl, valve of Leiblein.

offshoot of the *Paziella -Poirieria* line. *Paziella* is represented in the Recent fauna by a very few species, these occurring in the deeper waters of the tropical western Atlantic and the Galapagos. As Radwin and D'Attilio (1976) have synonymized several distinct phenotypes under the name *P. pazi*, it may be well to state that the two specimens used in this study are representative of the taxon in the strictest sense. Little is known of the biology of this species other than it inhabits the upper continental slope off eastern Florida and the Caribbean Sea.

Shell morphology: Shell small (to 35 mm), thin, biconical (Fig. 10). Protoconch (Fig. 17) of 1½ whorls, inflated, smooth. An outward flare of the lip and the first occurrence of axial growth striae mark the beginning of the teleoconch, which continues for up to 7 whorls. Spire angle 43–48°. Axial sculpture consists of 5–9 flaring varices per whorl, the number decreasing with increase in shell size. Each varix has a long open spine at the shoulder, and 1–2 shorter, recurved spines on the siphonal canal. Spiral sculpture comprised of 4–6 cords, each producing a short spine upon intersecting the varices. Suture impressed, shoulder rounded. Aperture ovate, deflected from the coiling axis by 10–15°. Siphonal canal open, dorsally deflected, equal in length to the aperture. Inner lip smooth, appressed along its entire length. Outer lip smooth, with only the spines flaring. Shell and aperture color white. Internal surfaces smooth and simple. The operculum (Fig. 11) is corneous, sharply ovate, terminally nucleate.

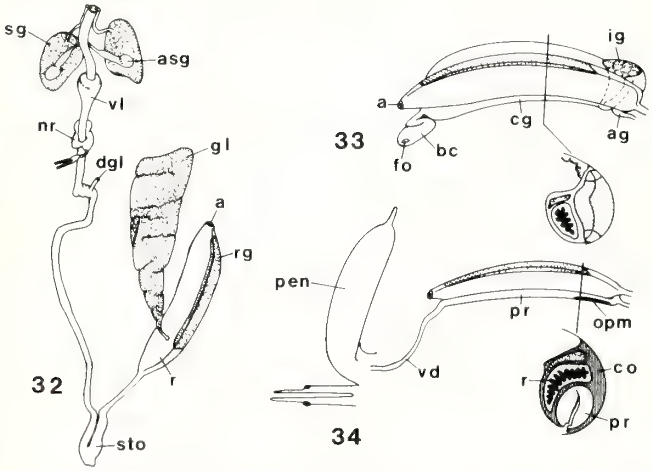
Animal—external features: The soft parts comprise 3¼ whorls, the digestive gland-gonad occupying 1¾ whorl, the kidney ¼ whorl and the mantle cavity spanning an entire whorl. Preserved animals are a light golden tan in color. The mantle edge is smooth, the tentacles very long and slender. The foot is squarish, with a deep, extremely glandular propodial groove and a small accessory boring organ.

Pallial complex: The mantle cavity is deep and narrow. The osphradium is long, narrow (L/W = 4), roughly symmetrical, with approximately 115 leaflets per side. The ctenidium is as wide as the osphradium and nearly twice as long, and has 180–200 deeply hanging triangular leaflets. The hypobranchial gland is slightly wider than the ctenidium and is nodular in appearance. The rectum and genital ducts are joined by connective tissue, and a simple, crested ridge can be discerned along the rectum. The pericardium is small, bordering the left rear corner of the mantle cavity. The adjacent kidney is large and has a pronounced nephridial gland.

Alimentary system: The alimentary system is similar to that of *B. aculeatus* in most regards. The radular ribbon (Fig. 27) is less than 0.1 times the shell length, and contains 168–172 rows of teeth (n = 2). The rachidian resembles that of *B. aculeatus*, but the cusps are less stout and are concentrated toward the center of the tooth. Lateral teeth resemble those of *B. aculeatus* but have proportionally longer cusps. The large, ovate valve of Leiblein (Fig. 32,vl) is bounded on either side by large, acinous salivary glands (Fig. 32,sg), the ducts from which are adherent to, but not embedded in the esophagus. Accessory salivary glands (Fig. 32,asg) are tubular, but each has a posterior "bladder" that is thin walled, nonglandular, and contains a clear, amber colored gel. The esophagus passes through the nerve ring (Fig. 32,nr) and under the gland of Leiblein (Fig. 32,gl). This gland consists of a highly folded glandular tube the empties into the esophagus via a duct (Fig. 32,dgl) anteriorly, and tapers posteriorly, ending in a clear ampulla. The esophagus continues posteriorly, paralleling the stomach (Fig. 32, sto) along its left side before entering it near its posterior limit. The intestine expands into a broad rectum (Fig. 32,r) when adjacent to the pallial gonoduct. An anal gland (Fig. 32,rg) runs along most of the length of the rectum. The anus (Fig. 32,a) is situated slightly anterior to the midlength of the mantle cavity,

Female reproductive system: The ovary and oviduct do not differ noticeably from those of the preceding species. The pallial oviduct contains an ingesting gland (Fig. 33,ig) that joins the albumen gland (Fig. 33,ag) near its juncture with the capsule gland (Fig. 33,cg). The bursa copulatrix (Fig. 33,bc) is muscular and triangular in outline. Dissection reveals it to be a simple S-shaped tube. Egg capsules and reproductive biology are unknown.

Male reproductive system: As in the preceding species, the testis lines the columellar side of the digestive gland, and the sperm travel via a simple, tubular testicular duct to the prostate gland (Fig. 34,pr). This gland extends along the posterior half of the mantle cavity, and communicates with it



Figs. 32–34. *Paziella pazi.* **32,** diagrammatic representation of the alimentary system, with the gland of Leiblein displaced to the right. **33,** the female pallial gonoduct, including a transverse section through the capsule gland, anal gland and rectum. **34,** the male pallial gonoduct, including a transverse section through the prostate gland, anal gland and rectum. a, anus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; co, connective tissue; dgl, duct of the gland of Leiblein; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; nr, nerve ring; opm, pallial opening of the prostate; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; sg, salivary gland; sto, stomach; vd, vas deferens, vl, valve of Leiblein.

along a short ventral slit (Fig. 34,opm). The prostate, together with the anus and anal gland, are surrounded by connective tissue (Fig. 34,co). The vas deferens (Fig. 34,vd) is not muscular as in the preceding species, and the penis (Fig. 34,pen) is broad and flat, tapering rapidly at its distal end without forming a papilla. The rapid taper may be an artifact of preservation.

Nucella lamellosa (Gmelin, 1791)
Figs. 12–14, 18, 28, 35–37)

This species was chosen for this study because of its superficial similarity to *T. geversianus*, both in shell morphology and in habitat. Shell morphology is extremely variable, and has been well documented by Kincaid (1957). Abbott (1974) provides a recent synonymy for this species. *Nucella lamellosa* is common intertidally and subtidally along the northwestern coast of North America.

Shell morphology: Shell large (to 82 mm), heavy, fusiform (Figs. 12–13). Protoconch (Fig. 18) of 1½ whorls, globose, pitted. Transition to teleoconch marked by onset of spiral sculpture. Teleoconch with up to 6½ inflated whorls. Spire angle 45–75°. Axial sculpture may be lacking in young or eroded specimens (Fig. 12), but more usually comprises 8–14 lamellae per whorl (Fig. 13). Spiral sculpture consists of 6–8 strong cords on the last whorl and 2 on the penultimate whorl. Suture appressed, shoulder rounded to tabulate. Aperture hemi-elliptical, deflected from the coiling axis by 20–25°. Siphonal canal about ½ as long as the aperture, open, axial or slightly deflected. Outer lip may be smooth and flaring or greatly thickened, with 5–7 denticles. Inner lip smooth, appressed along its entire length. Shell color ranges from pure white to orange and red, and may be solid or occur in spiral bands. Specimens with thin shells and prominent lamellae have smooth, topographically simple interiors, while heavy shelled individuals tend to have periodic internal thickening of the shell and pronounced apertural lirae every 120°. The operculum (Fig. 14) is thin, flexible, trapezoidal in outline and laterally nucleate.

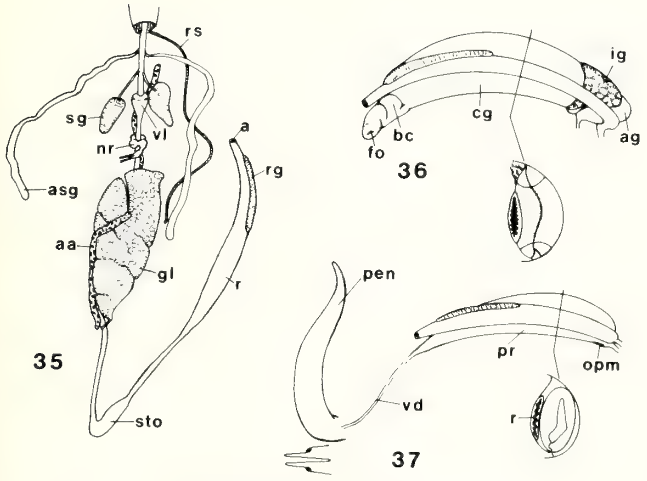
Animal—external features: The body consists of 2½ whorls: the mantle cavity spanning ½ whorl, the kidney ¼ whorl and the digestive gland-gonad 1½ whorls. Preserved animals were retracted ½ to ¾ whorl within the aperture and were uniformly light tan in color. The mantle edge is smooth, the siphon and tentacles are short. A large accessory boring organ is situated medially, just behind the deep propodial groove.

Pallial complex: The mantle cavity is short and broad. The osphradium is long, broad (L/W = 2.5) and roughly symmetrical, with 36–43 leaflets per side. The ctenidium is slightly wider than and twice as long as the osphradium and has about 200 leaflets. The hypobranchial gland, which produces a purplish secretion, is wider than the ctenidium and extends over the rectum and genital ducts. The rectum is adjacent to the genital ducts, but is not encapsulated with them by connective tissue. The pericardium, kidney and nephridial gland are similar to those of the preceding species.

Alimentary system: From the mouth, situated at the tip of a short, broad proboscis, an oral tube leads to the buccal cavity, which has the modified jaw in the usual position. The radular ribbon (Fig. 35,rs) is very long (0.4 shell length, n = 5) and contains 336–371 rows of teeth. The rachidia (Fig. 28) are broad, with the lateral posterior edges of the basal plate bifurcated, and with 3 long sharp cusps and 2 shorter cusps partially fused to the inner edges of the outer cusps. Lateral edges of the outer cusps have 3 serrate denticles. Lateral teeth each have a single, long, distally recurved cusp rising from a short basal area. Ducts of the normal salivary glands are embedded in the esophageal wall beneath the dorsal folds. Normal salivary glands (Fig. 35,sg) are reduced in size compared to the extremely large accessory salivary glands (Fig. 35,asg), which, when uncoiled, are half as long as the shell. Posterior to the valve of Leiblein (Fig. 35,vl) the esophagus passes through the nerve ring (Fig. 35,nr), is joined by a duct from the highly compacted gland of Leiblein (Fig. 35,gl), and proceeds to the tubular stomach (Fig. 35, sto). An anal gland (Fig. 35,rg) spans half the length of the rectum (Fig. 35,r).

Female reproductive system: The female reproductive system is similar to that of *P. pazi*, the major differences being that *N. lamellosa* has a larger ingesting gland (Fig. 36,ig) and a bursa copulatrix (Fig. 36,bc) with a blind muscular pouch. The ventral pedal gland is deep, being situated in the usual position.

Male reproductive system: The male reproductive system differs most notably from those of the preceding species



Figs. 35–37. *Nucella lamellosa*. **35,** diagrammatic representation of the alimentary system. **36,** the female pallial gonoduct, including a transverse section through the capsule gland and rectum. **37,** the male pallial gonoduct, including a transverse section through the prostate gland and rectum. a, anus; aa, anterior aorta; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; fo, female opening; gl, gland of Leiblein, ig, ingesting gland; nr, nerve ring; opm, pallial opening of the prostate; pen, penis; pr, prostate gland; r, rectum; rg, anal gland; rs, radular sac; sg, salivary gland; sto, stomach; vd, vas deferens; vl, valve of Leiblein.

having a convoluted testicular duct, a prostate gland with a large lumen, a thin, non-muscular vas deferens and a gradually tapering penis.

PHYLOGENY RECONSTRUCTION

Phenetics

Phenetic analyses of shell character data (Table 2) using UPGMA and Ward's method clustering produce the phenograms shown in figure 38. Both have the same topology, differ only in the morphological distance at which the final fusion is made, and, if interpreted as phylogenies, would support the hypothesis of a polyphyletic Trophoninae.

Cladistics

Character descriptions and analyses

Character 1. Cephalic tentacles:
(a) short, broad
(b) extremely long, narrow

Buccinaceans, volutaceans and non-muricine muricaceans possess short, broad tentacles. The increase in tentacle length observed in *Paziella pazi* also occurs in at least some other muricines (eg. *Murex acanthostephes* Watson, 1883, Abbott, 1972:157; *Chicoreus palmarosae* Lamarck, 1822, M. G. H.), and appears to be correlated with the presence of spines along the anterior portion of the shell. Elongated cephalic tentacles are considered to be a derived state.

Character 2. Osphradium:
(a) symmetrical
(b) dorsally expanded

Osphradia with an increased number of dorsally enlarged leaflets above the osphradial ganglion occur in *Trophon geversianus* and *Boreotrophon aculeatus* but not in other muricaceans studied nor in the Buccinacea or Volutacea, and are regarded as derived. This feature was not reported by Eales (1923) in her discussions of the anatomy of *Trophon shackletoni* Hedley, 1911 and *T. longstaffi* Smith, 1904, nor is it discernible in Taki's (1938) figure of the gross anatomy of *Boreotrophon alborostratus* Taki, 1938, but is very pronounced in *T. bahamondei* McLean and Andrade, 1982 (M.G.H.). The functional significance of this asymmetry is not known.

Character 3. Intermediate cusps of rachidia:
(a) free
(b) fused to outer cusps

Reduction in the number of cusps on the rachidian has been well documented in several rachiglossan lineages (Ponder, 1973). Although certainly convergent between these lineages, the possibility that it may be homologous within each lineage has yet to be investigated. One mechanism by which the number of cusps may be reduced is by fusion of cusps. This character state is provisionally considered to be derived.

Character 4. Major cusps of rachidia:
(a) long, slender
(b) short, broad

The more primitive members of Buccinacea and Volutacea have rachidia with numerous long, slender cusps of equal length. Reduction in the number of cusps and the shortening and buttressing of the remaining cusps are two trends that may be indicative of a shift from a raking to a gouging function of the rachidia. Both are considered to be derived traits.

Character 5. Lateral edges of rachidia:
(a) smooth
(b) denticulate

The presence of secondary denticles on the rachidian is uncommon in the Rachiglossa (Thiele, 1929), although less so in the Muricacea (Radwin and D'Attilio, 1976), where it appears to be restricted to the Thaididae, Ocenebridae and, to a lesser extent, the Muricopsinae. The presence of denticles is interpreted as a derived condition, although it may not be homologous in all of these groups.

Character 6. Posterio-lateral edge of rachidian basal plate:
(a) simple
(b) with bifid edges

The bifid condition is prevalent throughout the Thaididae (Wu, 1965; Kool, personal communication) and also occurs, although not necessarily in homologous form, in the Ocenebrinae and Muricopsinae, but has not been reported outside the Muricacea. It may function as an interlocking mechanism for rachidia and/or lateral teeth. Its presence is considered a derived state.

Table 2. Measurements of shell characters presented in the format Mean/Standard Deviation. All linear measurements are in mm. The mean values constitute the data matrix for phenetic analysis.

Character	*T. geversianus* (n = 10)	*B. aculeatus* (n = 10)	*P. pazi* (n = 5)	*N. lamellosa* (n = 10)
1. Sbc	1.35/0.04	1.88/0.05	1.74/0.07	1.53/0.13
2. Ssc	2.23/0.14	6.41/0.51	5.24/0.31	2.44/0.23
3. Rsl	0.54/0.03	1.14/0.07	1.19/0.09	0.56/0.03
4. beta	2.5°/0.11°	14.7°/1.99°	9.5°/0.88°	-7.3°/0.91°
5. W	2.11/0.31	1.41/0.21	1.29/0.42	1.70/0.22
6. theta	22.8°/3.1°	25.2°/1.08°	20.6°/0.81°	18.3°/1.77°
7. D	0.127/0.01	0.216/0.03	0.175/0.02	0.089/0.01
8. T	3.56/0.15	5.82/0.21	5.02/0.18	4.53/0.21
9. L	52.6/15.1	30.1/4.8	30.9/8.8	54.7/13.2
10. W/L	0.62/0.05	0.31/0.02	0.41/0.01	0.51/0.03
11. AL/L	0.44/0.03	0.26/0.02	0.27/0.01	0.34/0.02
12. # whorls	5.2/0.8	8.6/0.4	6.6/1.2	5.6/0.4
13. # var	18.5/2.0	12.1/0.9	5.8/0.4	10.3/1.2

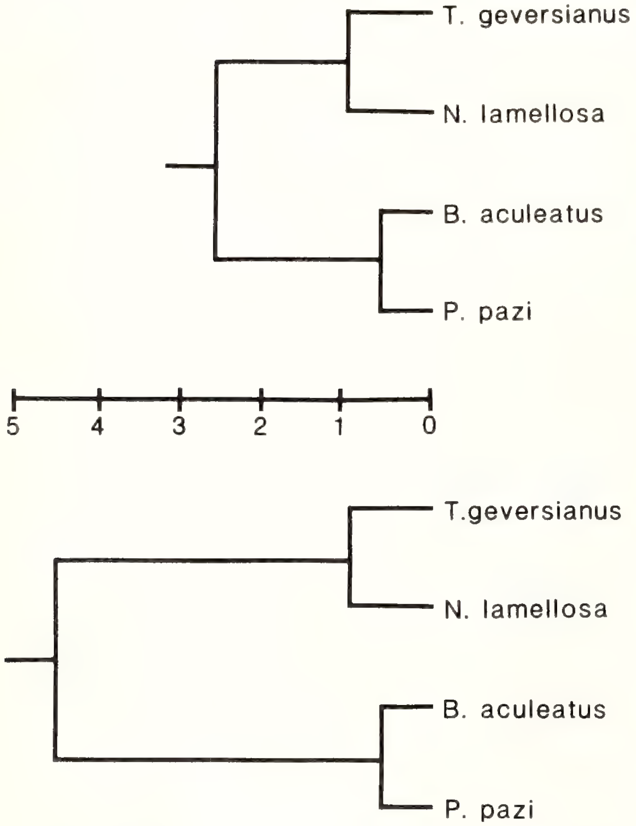


Fig. 38. Phenograms based on UPGMA (upper) and Ward's Method (lower) cluster analyses of morphological distance.

Character 7. Basal plates of lateral teeth:
(a) with broad attachment area
(b) with narrow attachment area

A decrease in the number of cusps on the lateral teeth has occurred independently in at least 8 rachiglossan lineages (Ponder, 1973). In the Muricacea, this has resulted in a monocusped condition, with a long cusp along the outer edge of the basal plate. This scythe-like configuration, here considered a synapomorphy uniting all Muricacea, is nevertheless primitive within the group and suggests a piercing, slicing function. Reduction and concentration of the attachment area would increase the flexibility of the tooth about the cusp axis, which would be more useful if the tooth were to assume a grappling function.

Character 8. Accessory salivary glands:
(a) longer than and free of salivary glands
(b) shorter than and embedded in salivary glands

The polarity of this transformation is based on the tendency within Rachiglossa toward loss of the accessory salivary gland. Total loss has occurred in all Buccinacea, in several volutacean families (Ponder, 1973) as well as in one muricacean family (Ward, 1965; Ponder, 1973) and several muricid genera (Wu, 1973; Carriker, 1981). Within the Volutidae, large free accessory salivary glands are found in the most primitive subfamily (Volutinae), becoming smaller and embedded in the salivary glands in the more advanced subfamilies (Zidoninae and Odontocymbiolinae) (Clench and Turner, 1964).

Character 9. mid-esophagus:
(a) simple, tubular
(b) greatly expanded, dorsally recurved

The mid-esophagus, which extends from the valve of Leiblein to the duct of the gland of Leiblein, is simple and tubular in most Buccinacea and Volutacea. Within Muricacea this area exhibits varying degrees of expansion and elongation (Ponder, 1973). Ponder (1973) reported that the dorsal folds have been stripped from the mid-esophagus by the fusion of their apices in the trophonine *Xymene ambiguus* (Philippi, 1844).

In *Trophon geversianus* and *T. bahamondei* (M.G.H.), this section becomes greatly expanded and increases in length, forming a dorsal loop (Fig. 21,hl). It is considered likely that the "coiled caecum" reported in *T. shackletoni* and *T. longstaffi* (Eales, 1923) corresponds to this structure. The presence of this feature in austral species of *Trophon* is considered a derived feature.

Character 10. Stomach with:
(a) broad posterior mixing area
(b) reduced posterior mixing area

The widespread occurrence of broad posterior mixing areas or caeca in Muricacea (Graham, 1949; Wu, 1965; Smith, 1967; Ponder, 1973), Buccinacea (Brock, 1936; Smith, 1967; Ponder, 1973) and to a lesser extent in Volutacea (Ponder, 1973) is regarded as representing the primitive state. The tendency for the neogastropod stomach to become U-shaped and tubular has been discussed at length by several authors (Graham, 1949; Smith, 1967) and this condition is considered to be derived.

Character 11. Anal gland:
(a) present
(b) absent

The widespread if sporadic occurrence of an anal gland in muricacean, volutacean and certain toxoglossan families suggests that its presence may be regarded as a primitive state. Its loss in such diverse taxa as Buccinacea, Magilidae and Vasinae is a derived condition convergent between but homologous within each taxon.

Chapter 12. Separate sperm ingesting gland:
(a) present
(b) absent

A separate sperm ingesting gland has been reported in some but not all members of the 3 superfamilies of Rachiglossa (Ponder, 1973). Houston (1976) reported this structure lacking in 2 trophonines and one ocenebrine but present in 7 other muricacean taxa. The loss of this gland is regarded as a derived state. Its function has likely been taken over by another portion of the pallial gonoduct.

Chapter 13. Position of the rectum relative to the prostate gland:
(a) medial
(b) dorso-lateral
(c) dorsal, both enclosed in connective tissue

The rectum is medial to the female pallial gonoduct in all rachiglossans studied, and a similar arrangement in males is provisionally regarded as a primitive state. The migration of the rectum to a dorso-lateral and ultimately to a dorsal position is interpreted as representing progressively more derived conditions. The enclosure of both organs in connective tissue in Trophoninae may serve to increase the height of the mantle cavity.

Character 14. Vas deferens:
(a) thin, tubular
(b) thick, muscular

The thick, muscular condition of the vas deferens, found in *Trophon geversianus, T. bahamondei* (M.G.H.) and *Boreotrophon aculeatus*, is distinctive, and has not been reported in other rachiglossans. Presence of this modification is regarded as a derived trait.

Character 15. Penis tip with terminal papilla:
(a) present
(b) absent

Within the Muricacea, penial papillae have not been reported outside the Trophoninae (Wu, 1973; Houston, 1976), and their presence is regarded as a derived condition. Similar structures are found in Buccinacea, and can be attributed to convergence.

Cladistic analysis of the 15 anatomical and radular characters, comprising 31 character states, listed in Table 3 produced the cladogram in figure 39. The cladogram required 19 changes of character state, of which 3 (characters 3, 7, 10) occurred twice, and are interpreted as being convergent. Open circles, labelled A, B, and C, represent hypothetical ancestors, and correspond to the ancestral trophonine, muricid and muricacean respectively. Reconstructed phenotypes of these hypothetical ancestors are included in Table 3.

Character compatibility analysis of the anatomical data yielded 2 cliques of mutually compatible characters (Table 4). The largest, Clique I, is supported by 13 characters and is compatible with the cladogram in figure 39. The smaller, Clique II, is supported by 8 characters, and is compatible with the arrangement produced by the phenetic analyses. It should be noted, however, that 5 characters (1, 5, 6, 9, 11) are non-discriminating, and would support any phylogenetic arrangement of the 4 taxa.

DISCUSSION

Phenetic analyses of shell character data cluster *Trophon geversianus* with *Nucella lamellosa* and *Boreotrophon aculeatus* with *Paziella pazi*, raising the question, are these similarities indicative of phylogenetic relationships or of convergent responses to habitat. The relationship between shell morphology and habitat has been convincingly demonstrated by Davis (1979) in Pomatiopsidae, and similar convergence is known to occur in other gastropods (eg. Buccinacea, Ponder, 1973; shelled opisthobranchs, Gosliner, personal communication). If shell morphology is significantly influenced by habitat, one would expect species that are sympatric over part of their ranges to be more similar than species inhabiting similar habitats a hemisphere apart. Although considerably more data are required to seriously evaluate this hypothesis, the data from this study at least conform to its prediction.

The most parsimonious cladogram generated by the Wagner algorithm (Fig. 39) is congruent with the largest clique of mutually compatible characters. Further support for this phylogenetic arrangement is provided by the fossil record. The Thaididae, here considered the most primitive of the taxa studied, is also the oldest, dating back to the Albian stage of the Upper Cretaceous (Sohl, 1969; Taylor et al., 1983). *Paziella*, the oldest of the muricid genera, first appears in the Cenomanean stage (Vokes, 1970), while Trophoninae, the youngest and most specialized of the taxa under investigation, is first reported from the Eocene (Wenz, 1941).

The 3 characters (2 radular, 1 stomach) that are incongruent with this cladogram all have identical distributions. Changes in polarization of their transformation series do not improve their compatibility. Wu (1965a) considered the bifid edges of thaidid rachidian teeth to consist in part of laterally displaced outer cusps. Under this interpretation, the fused intermediate cusps of *Nucella lamellosa* would be denticles, and not homologous to the fused intermediate cusps of *Trophon geversianus*. In light of the numerous, well documented (Ponder, 1973) instances of convergence in rachiglossan radular morphology, it is likely that these presumed synapomorphies are, in fact, due to convergence. It also appears likely that changes in stomach morphology are not homologous.

Many of the characters that support the proposed phylogenetic arrangement pertain to the reproductive systems, which are "more conservative and useful in determining systematic arrangements" (Wu, 1973).

The morphologies of the egg capsules of 3 of the species in this study are unknown. Nevertheless, it should be noted that two different types of egg capsules occur in the Trophoninae. Most species studied have primitive, lenticular capsules (Bandel, 1976), but species of *Trophon s.s.* produce stalked capsules (Fig. 23) similar to those of Thaididae and Ocenebrinae.

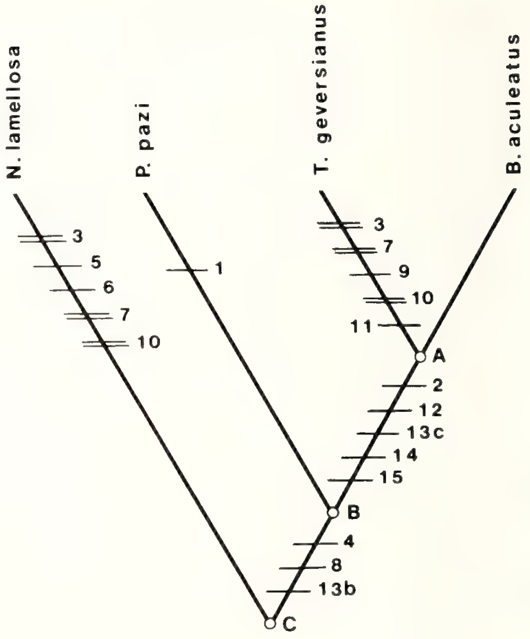


Fig. 39. Wagner reconstruction of phylogenetic relationships of muricacean taxa. Open circles represent hypothetical ancestors. Single slashes across tree branches signify transformation of the corresponding character from the primitive to the derived state. Double slashes indicate character transformations that occur more than once.

Examination of figure 39 reveals that both deep-water species (*P. pazi* and *B. aculeatus*) differ little if at all from their

Table 3. Character state distributions of qualitative anatomical characters. A, B and C represent reconstructed phenotypes of hypothetical ancestors.

Character	*T. geversianus*	*B. aculeatus*	*P. pazi*	*N. lamellosa*	A	B	C
1.	a	a	b	a	a	a	a
2.	b	b	a	a	b	a	a
3.	b	a	a	b	a	a	a
4.	b	b	b	a	b	b	a
5.	a	a	a	b	a	a	a
6.	a	a	a	b	a	a	a
7.	b	a	a	b	a	a	a
8.	b	b	b	a	b	b	a
9.	b	a	a	a	a	a	a
10.	b	a	a	b	a	a	a
11.	b	a	a	a	a	a	a
12.	b	b	a	a	b	a	a
13.	c	c	b	a	c	b	a
14.	b	b	a	a	b	a	a
15.	b	b	a	a	b	a	a

Table 4. Memberships of cliques of mutually compatible characters.

Clique	Membership
I	1b,2b,4b,5b,6b,8b,9b,11b,12b,13b,13c,14b,15b
II	1b,3b,5b,6b,7b,9b,10b,11b

immediate ancestors, while the shallow-water species (*T. geversianus* and *N. lamellosa*) have each undergone transformations in several characters. These observations are in agreement with the onshore-innovation, offshore-archaic evolutionary model discussed by Jablonski et al. (1983).

The results of this study support the following reconstruction of muricacean phylogeny. The Thaididae are probably the most primitive and, together with the Rapanidae, the most ancient members of the superfamily, and should be accorded a status equal to that of the Muricidae. The family Muricidae is morphologically the most advanced of the muricacean families (the Magilidae, geologically slightly younger than the Muricidae, are here considered to be a specialized offshoot from either the thaidid or rapanid lines). Within Muricidae, *P. pazi* more closely resembles the ancestral muricid phenotype (Ancestor B) than any trophonine, and it is suggested that Muricinae is the most primitive of the muricid subfamilies. The Trophoninae comprise a comparatively recent monophyletic group characterized by unique specializations of the osphradium and reproductive organs.

Finally, it is noted that the characters upon which virtually all trophonine taxonomy is based (i.e.—shell and radular characters) are most subject to convergence, and are less reliable as systematic characters than has been previously realized. In light of this information, reassignments of trophonine genera to Thaididae based on radular characters should be reappraised.

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HISTOLOGICAL AND HISTOCHEMICAL STUDIES ON THE FOOT AND MANTLE OF *CIONELLA LUBRICA* (MUELLER) (GASTROPODA: PULMONATA)

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ABSTRACT

The foot of *Cionella lubrica* is lined by a simple ciliated columnar epithelium. Pedal glands composed of large spherical cells that secrete acid mucopolysaccharides line the lateral margins of the foot. Muscle fibers are few and randomly arranged.

The surface of the mantle is composed of a cuboidal epithelium. Within the mantle are large spherical cells that contain primarily acid mucopolysaccharides, large ovoid cells that contain acid mucopolysaccharides and glycogen, and small spherical cells that contain glycogen, acid mucopolysaccharides, and some protein.

The structure of the foot and mantle of the Mollusca has received considerable attention. Among pulmonate gastropods, the histological details of the mantle and/or foot of generally well-known species such as *Arion ater, Helix pomatia, H. aspersa, Anguispira alternata,* and *Discus rotundatus* have been investigated by Barr (1927), Baecker (1932), Campion (1961), Jones (1953), and Elves (1961), respectively. In these reports, the various types of cells, glands, and secretions are elucidated. Stasek and McWilliams (1973) provide an overview of the gastropod mantle in their summary of the evolution and morphology of the molluscan mantle edge. Biochemical and histochemical aspects of molluscan tissues are summarized by Goudsmit (1972), Hyman (1967), and Voogt (1972).

Cionella lubrica (Mueller) is a small (5–7mm) pulmonate inhabiting leaf litter throughout most of the continental United States. As far as can be determined, little has been reported concerning the biology of this snail. Gugler (1973) has studied the reproductive anatomy of *C. lubrica,* while van Es and Boag (1981) mention *C. lubrica* in their study of the terrestrial snails of central Alberta, Canada.

The intent of this study is to add to our knowledge of this little-known snail. Not only is a description of the aforementioned tissues of *Cionella lubrica* presented, but the information obtained by this histological and histochemical approach is related to the biology of *C. lubrica* in terms of locomotion, protection, and respiration.

MATERIALS AND METHODS

Specimens of *Cionella lubrica* were collected from the southeastern corner of the Fremont State Lakes Recreation Area, Dodge County, Nebraska, U.S.A. Laboratory populations were maintained at room temperature in plastic boxes (16.5 × 30.0 × 8.5 cm) with a 3–5 cm substratum of sandy loam soil. Sufficient water was added to maintain high humidity within the boxes.

Adult (5–7 mm) snails were narcotized in a solution of 50 cc water, 5–10 cc 70% ethyl alcohol, and 5-10 drops propylene phenoxytol. When the snails were fully relaxed, the shell was mechanically removed with fine forceps. Whole specimens were fixed as noted below and embedded in either paraffin (melting point 54° C.) or, in order to visualize lipids, in a 9.5 to 0.5 mixture of Carbowax compounds 4000 and 1540. All specimens were serially sectioned.

For general histology Bouin's-fixed material was sectioned at 8 μm and stained with Harris' hemotoxylin and eosin.

The following histochemical techniques, with the appropriate controls as noted in the references, were used:

Nucleic acids. Bouin's-fixed material was sectioned at 8 μm and stained with the Feulgen reaction (McManus and Mowry, 1965) to visualize chromatin. RNA and DNA were distinguished with the methyl green-pyronin test (Murgatroyd, 1963) on Carnoy's-fixed sections (8 μm).

Proteins. All specimens were sectioned at 4–5 μm. Specimens were fixed in Bouin's for the mercury-bromphenol blue method (Humason, 1972) to demonstrate basic proteins and for the Millon reaction (Humason, 1972) to distinguish protein rich in tyrosine. For the Deitch modification of the Sakaguchi reaction (Humason, 1972) to visualize arginine-rich protein, specimens were fixed in absolute ethyl alcohol-glacial acetic acid (3:1).

Carbohydrates. All specimens were fixed in Rossman fluid and sectioned at 8 μm. Mowry's modification of the

Hale reaction (McManus and Mowry, 1965) and Alcian blue-kernechtrot (pH 2.5) (Humason, 1972) demonstrated the distribution of acid mucopolysaccharides. To distinguish acid and neutral mucopolysaccharides the Alcian blue-periodic acid Schiff (PAS) (pH 2.5) technique (McManus and Mowry, 1965) was employed. Kramer and Windrum's (1955) Azure A technique visualized sulfated mucopolysaccharides. Glycogen was demonstrated by the alcoholic PAS reaction (Humason, 1972).

Lipids. Formalin-fixed material was sectioned at 8 μm and stained with oil Red 0 in isopropanol (Humason, 1972).

Phosphatases. Material was fixed according to DeNicola (1949), sectioned at 8 μm, and stained according to Gomori's cobalt method for alkaline phosphatases and Gomori's method for acid phosphatases (McManus and Mowry, 1965).

RESULTS

Histology

The outer integumental layer of the foot was composed of a high (18 μm × 5 μm) simple ciliated columnar epithelium. The nuclei of these cells were large and contained two or three nucleoli. The epithelium was subtended by a thin basement membrane. There was no apparent change in the composition of this epithelium along the antero-posterior axis of the foot. The surface of the foot was smoother in its anterior aspect than in its more posterior regions, but no distinct grooves were seen.

The connective tissue fibers of the foot interior, which are of basic protein, were loosely arranged near the surface of the foot and more densely arranged deeper within the foot. The fibroblasts were small (5 μm). Their nuclei contained two or three nucleoli. Small blood spaces were numerous and evenly distributed throughout the length of the foot. Along the length of the lateral margins of the foot were a few large (25–30 μm) spherical cells that occurred in clusters of five and six. These cells formed a series of glandular apparatuses, i.e., pedal glands, each of which releases its contents by a common pore (Fig. 1). In some areas, particularly in the middle region of the foot, these same cells occurred singly. Muscle fibers were few and randomly arranged.

The mantle epithelium was composed of 7–8 μm cuboidal cells (Fig. 2). The nuclei of these cells were large and contained two to four nucleoli. A distinct basement membrane was not evident.

Blood spaces of the mantle were fewer and considerably larger than those of the foot. The interior of the mantle within the two epithelial layers was composed primarily of groups of large spherical (25–40 μm) and ovoid (25 μm × 50 μm) cells with small (10 μm) spherical cells scattered amongst the larger cells. The nuclei of the larger cells contained one or two nucleoli. Groups of large cells formed glands, emptying their contents by a common pore to the outer mantle surface (Fig. 3). In some cases, these cells occurred as unicellular glands.

Histochemistry

The integumental cells of the foot and mantle of *C. lubrica* were quite similar in their staining characteristics. Arginine-rich protein was mildly evident in the cytoplasm of these cells; tyrosine-rich protein was absent. The mercury-bromphenol blue reaction revealed a distinct layer of basic protein near the apical end of both integumental cell types (Fig. 4). The carbohydrate stains were uniformly negative, save for an indication of a small amount of sulfated acid mucopolysaccharide in the mantle integument. The stains for alkaline and acid phosphatases and for lipids likewise were negative.

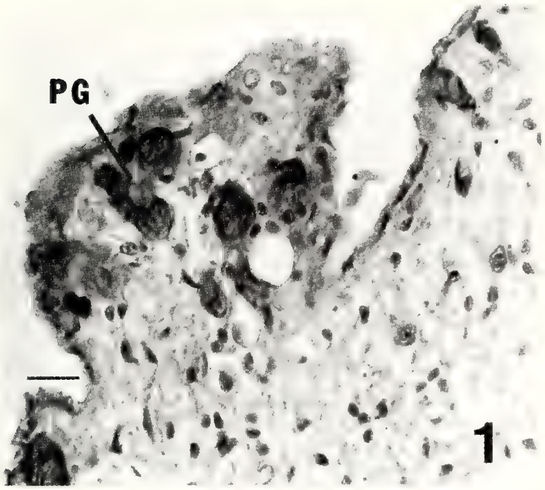
The staining results for the glandular cells of the foot and mantle are summarized in Table 1. The most conspicuous positive results were for the carbohydrate stains. Acid mucopolysaccharides were more plentiful than neutral mucopolysaccharides. Glycogen was found only in the large ovoid cells and small spherical cells of the mantle (Fig. 5), while sulfated acid mucopolysaccharides were found only in the small spherical cells of the mantle. A small amount of protein was evidenced in some mantle cells. Alkaline phosphatase was abundant in the glandular cells of the foot and mantle, but acid phosphatase was found only in the large ovoid and small spherical cells of the mantle. There was no evidence of lipid in any of the glandular cells.

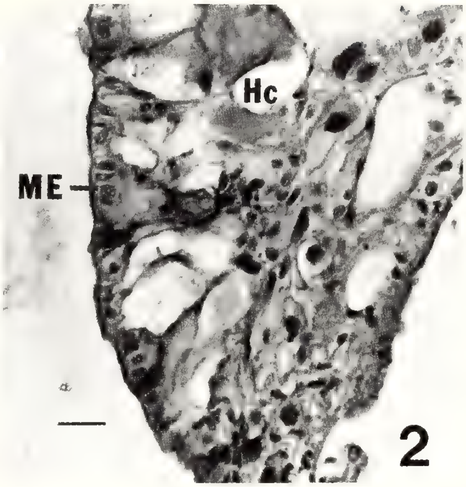
DISCUSSION

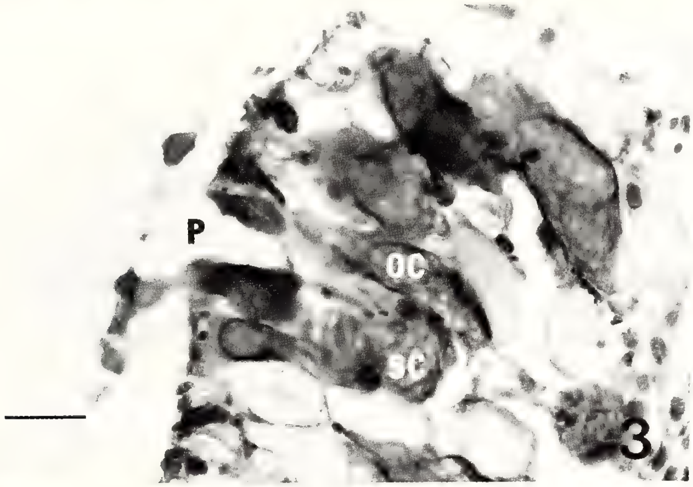
The integumental covering of the foot of *Cionella lubrica* is not unlike that of other Mollusca. A ciliated columnar epithelium that is interspersed with gland cells, or goblet cells, has been found covering the foot of gastropods (Albanese-Carmignani and Calabro, 1978; Baecker, 1932; Barr, 1927; Campion, 1961; Elves, 1961; Morton, 1955a, 1955b; and Skidmore and Rivera, 1982), amphineurans (Cowden, 1963), and bivalves (Sullivan, 1961). Differences lie primarily in cell and nucleus size and cilia length. It appears then that the integument of the foot of *C. lubrica* conforms rather closely to a general molluscan model.

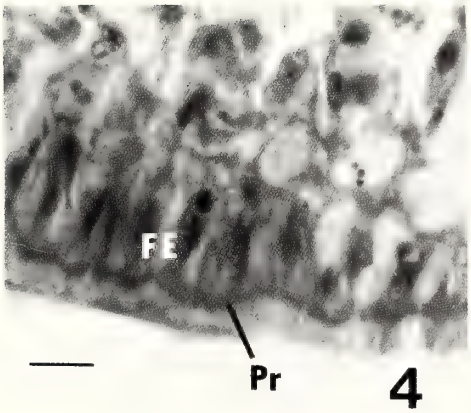
The connective tissue and musculature of the foot of *Cionella lubrica* is similar to that described by Morton (1955a) for *Otina otis* and to that of *Discus rotundatus* and *Lymnaea peregra* (= *Radix peregra*) as described by Elves (1961). This histology, together with the number of mucus-secreting cells seen in *C. lubrica* is consistent with the view of Elves (1961) of a small snail that utilizes primitive ciliary locomotion on well-lubricated surfaces.

The foot of the primitive pulmonate *Melampus bidentatus* has distinct transverse grooves and large blood spaces in the propodium and smaller blood spaces in the metapodium (Moffett, 1979). Observations of living *Cionella lubrica* indicate that it does not lift the anterior foot in a *M. bidentatus*-like "crawl-step." Since the foot of *C. lubrica* lacks transverse grooves and its blood spaces are small throughout the length of the foot, there appears to be a correlation between crawling mode and foot histology.









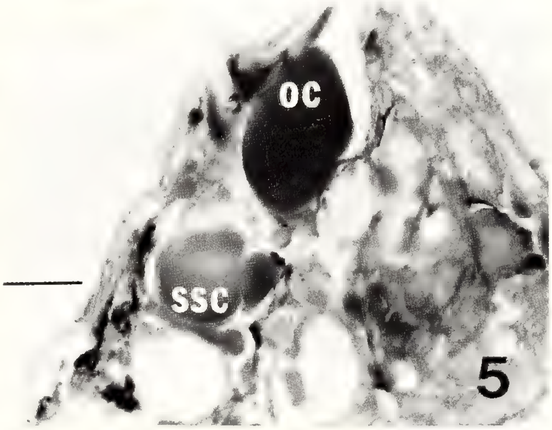


Fig. 1. Foot of *Cionella lubrica*, showing the cells of the pedal glands (PG) and their acid mucopolysaccharide contents. Alcian blue-kernechtrot. Scale bar = 25 μm. **Fig. 2.** Mantle of *Cionella lubrica*. ME = mantle epithelium, Hc = hemocoel. Alcian blue-kernechtrot. Scale bar = 25 μm. **Fig. 3.** Mantle of *Cionella lubrica*, revealing the pore (P) of a group of gland cells. OC = ovoid cell, SC = spherical cell. Alcian blue-kernechtrot. Scale bar = 25 μm. **Fig. 4.** Integument of the foot of *Cionella lubrica*. Note the layer of basic protein (Pr) on the apical surface of the foot epithelium (FE). Mercury-bromphenol blue. Scale bar = 10 μm. **Fig. 5.** Mantle of *Cionella lubrica'* indicating the presence of glycogen in the ovoid cells (OC) and small spherical cells (SSC). Alcoholic PAS. Scale bar = 25 μm.

Table 1. Histochemical reactions of the glandular cells of the foot and mantle of *Cionella lubrica*.

		Foot	Mantle		
Stain	To demonstrate	Large spherical cells	Large spherical cells	Large ovoid cells	Small spherical cells
Hale Reaction	Acid mucopolysaccharide	+ + +	+	+	+
Azure A	Sulfated acid mucopolysaccharide	−	−	−	+
Alcoholic PAS	Glycogen and other carbohydrates	−	−	+ + +	+ +
Alcian blue-PAS	Acid mucopolysaccharide	+	+ + +	+ +	−
	Neutral mucopolysaccharide	−	+	+	+ +
Alcian blue-kernechtrot	Acid mucopolysaccharide	+ +	+ +	+ +	+
Mercury—bromphenol blue	Basic protein	−	−	−	+
Sakaguchi reaction	Protein-bound arginine	−	−	+	+
Millon reaction	Tyrosine-rich protein	−	−	−	−
Alkaline phosphatase	Active transport	+ +	+ +	+ +	+ +
Acid phosphatase	Holocrine secretion and glycogen formation	−	−	+ +	+ +
Oil Red 0	Lipid	−	−	−	−

(−) = negative reaction, (+) = mild positive reaction, (+ +) = strong positive reaction, (+ + +) = very strong positive reaction.

There is little in the literature that comments upon the histochemical nature of the epithelial cells of the gastropodan foot. Albanese-Carmignani and Calabro (1978) show the presence of basic protein, protein with S-S groups, and tyrosine in the foot of the prosobranch *Pisania maculosa.* Since the basic protein in the integumental cells of *Cionella lubrica* occurred in such a distinct layer near the apical surface of the cells, this protein may serve as a mechanical support for the cells. The absence of alkaline and acid phosphatases would indicate that these proteins are not secreted. Similar observations can be noted for the mantle epithelium.

Various types of mucus-secreting cells in the foot of mollusks have been described. In most gastropods these cells are grouped to form pedal, suprapedal, hypobranchial, or caudal glands, with singular cells often located subepidermally or occasionally intraepidermally. The arrangement of the cells in *Cionella lubrica* is similar to that seen in the opisthobranch *Unela nahantensis* as figured by Doe (1974), although *C. lubrica* lacks the well-defined anterior pedal gland of *U. nahantensis* described by Robinson and Morse (1979).

Acid mucopolysaccharide has been found commonly in the mucous cells of the foot of gastropods (Albanese-Carmignani and Calabro, 1978; Campion, 1961; Robinson and Morse, 1979; and Skidmore and Rivera, 1982), bivalves (Cranfield, 1973 and Sullivan, 1961), and amphineurans (Cowden, 1963). The mucous cells of *Cionella lubrica* are somewhat large relative to the size of this diminutive snail. It should be mentioned here that there is little conformity among gastropods relative to body size and mucous cell size. In point, Elves (1961) figures mucous cells of *Discus rotundatus* as being smaller than those of *C. lubrica,* while the cells of *Helix aspersa* are considerably larger (Campion, 1961). The significance of the range of sizes is tentative at best. For *C. lubrica,* at least, the large size is indicative of the volume and the importance of the secretion. As far as the mucus itself is concerned, it would seem that *C. lubrica* conforms to a rather general molluscan condition. As in other mollusks, certainly this mucus functions in locomotion for lubrication and adhesion. Morton (1955b) implicates the mucus of the pulmonate *Leucophytia bidentata* in food ingestion. *C. lubrica,* however, lacks a large supra-pedal gland and it is doubted that the mucus performs this food-getting function in *C. lubrica.* As in *H. aspersa* where some of the mucous glands lack musculature (Campion, 1961), the foot glands of *C. lubrica* would appear to empty their secretions by relying upon changes in hemocoel pressure.

Campion (1961) and Morton (1955b) describe a ciliated, or at least partially ciliated, columnar epithelium for the mantle of the pulmonates *Helix aspersa, Otina otis,* and *Leucophytia bidentatus,* respectively; likewise, the prosobranch *Pisania maculosa* has a ciliated columnar epithelium lining the outer mantle (Albanese-Carmignani and Calabro, 1978). The integument of the mantle of *Cionella lubrica* was more like the cuboidal to low columnar epithelium of the pulmonate *Anguispira alternata* described by Jones (1935), although "spherical basal cells" were not evidenced in *C. lubrica.* The proximity of the large hemocoels of the mantle to this relatively thin epithelium certainly facilitates respiration in *C. lubrica.*

The gland cells of the mantle of *Cionella lubrica* secrete a mucus that is both neutral and acid. The appearance of these cells is rather like that of the terrestrial prosobranch *Pomatias elegans* as described by Storch and Welsch (1972) in which the secretory area is a structureless mass traversed by narrow bands of dense cytoplasm (see Fig. 3). Neutral mucopolysaccharide has been found in the mantle glands of the prosobranch *Pisania maculosa* by Albanese-Carmignani and Calabro (1978) and in *Busycon carica* and *B. canaliculatum* by Walsh (1981). Acid mucopolysaccharide production by mantle glands has been noted for a variety of mollusks (Campion, 1961; Hillman, 1968; Love and Frommhagen, 1953; Morton, 1955b; Prezant, 1978; and Sullivan, 1961). Judging from the number of these glands in the mantle of *C. lubrica* it would seem their secretion plays an important role in assisting in locomotion. It seems reasonable to also speculate that this mucus may aid in skin respiration by keeping integumental surfaces moist (Barr, 1927; Barrett, 1970; Fretter, 1943). This mucus would also help prevent dessication (Barrett, 1971 and Storch and Welsch, 1972). The glycogen in the large ovoid cells of the mantle may represent a nutrient store for estivating or hibernating snails.

Cranfield (1973) notes that the amount of protein in mucus may have distinct effects on its properties, and thus on its function. The amount of protein, produced mostly by the small spherical cells, in the mantle of *Cionella lubrica* is apparently small and what effects it may exert have not been specifically identified in this study. However, as Campion (1961) suggests for *Helix aspersa,* it could be that this protein plays a role in the formation of the epiphragm and in making the mucus less viscous so it runs off the integument, taking potential irritants with it.

Fretter (1943) associates the mucus from the marginal glands of the mantle of the pulmonate *Onchidella celtica* with a repugnatorial function. Perhaps the sulfated acid mucopolysaccharide from the small spherical cells in the mantle of *Cionella lubrica* may serve this purpose. However, biochemical, ecological, and behavioral studies will be required before this kind of protection can be confirmed.

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AERIAL EXPOSURE IN THE GENUS *CREPIDULA* (GASTROPODA: PROSOBRANCHIA) WITH COMPARISONS TO OTHER TAXA

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ABSTRACT

Three species of *Crepidula* (Gastropoda: Prosobranchia), which live in different habitats with different exposures to desiccation, have different behavior patterns when exposed to air. The relative resistance of the species to desiccation in the laboratory was tested. *C. fornicata* was observed in the field to lift its shell from the substratum (gape) when out of water, and in the laboratory had the lowest ability to tolerate water loss as a percent of body weight, as well as the most rapid water loss per body weight. Exposed *C. convexa* remains clamped against the substratum in nature, retaining water in the mantle cavity. It had the highest tolerance to desiccation in the laboratory and a very low rate of water loss. Limited data for *C. plana* suggest that it was intermediate in the first respect. At Cape Cod, Massachusetts, *C. convexa* and *C. plana* are often found intertidally, although *C. plana* lives in moist microhabitats. *C. fornicata* is rarely intertidal. Therefore, differences in physiology are correlated with habitat differences, although the direction of causality remains unproven. Gaping as a response to exposure to air is characteristic of several mollusks.

Crepidula fornicata (Linnaeus), *C. convexa* Say, and *C. plana* Say are filter-feeding prosobranch gastropods found sympatrically in shallow water along the Atlantic Coast of North America. They differ in preference for substratum and microhabitat (Coe, 1942). *C. convexa* often lives on the shells of live mollusks or hermit crabs and frequently occurs intertidally. *C. plana* preferentially occupies inner surfaces of dead shells that are occasionally occupied by hermit crabs that venture into the intertidal zone. The relative humidity of such an internal shell environment is high compared with the habitat of intertidal specimens of *C. convexa*. *C. fornicata* is primarily subtidal; when found living above mean low tide, it is usually submerged in tide pools (Hoagland, 1979).

This paper reports on (1) field and laboratory observations of the behaviors of these three species when exposed to air in the vicinity of Woods Hole, Massachusetts, and (2) experiments comparing the species' abilities to retain water and to survive desiccation. These results for the species of *Crepidula* are compared with available information on littoral mussels and limpets.

METHODS

The three species of *Crepidula* taken from waters 0–1 m below low water at Vineyard Haven, Martha's Vineyard and Penzance Point, Woods Hole, Massachusetts, were observed in addition to specimens of each species that had been cast up higher on the beach by storms or that were attached to other organisms that had carried them into the intertidal zone. *C. fornicata* was found on the horseshoe crab *Limulus polyphemus*, *C. convexa* was on *Littorina littorea*, and *C. plana* was inside *Lunatia heros* shells that contained hermit crabs. All three species were also found subtidally on small stones, old bottles, and dead shells.

Specimens of each species were brought onto water tables at the Woods Hole Oceanographic Institution still attached to their substrata and maintained at ambient temperatures (18 to 25° C). Supplemental food consisting of *Isochrysis galbana* and *Monochrysis lutheri* was added once a week. Experiments were run in July after 2 weeks' acclimation.

To observe gaping behavior, snails still attached to their substrata, representing all sex categories (juvenile, male, female, female brooding eggs, and animal in the process of changing sex from male to female) were removed from the water tables. They were exposed to air at room temperature (22–26° C). The shell length of each animal was measured with calipers. The animals were examined at 30-minute intervals for 24 hours, and subsequently at one-hour intervals. When an individual lost its grip on the substratum and failed to contract its head and tentacles when

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touched with a dissecting needle, it was considered to be moribund and returned to sea water. If it recovered after 48 hours, it was not included in the data. Survival time for each animal that did not recover was recorded as the last time it was observed alive. Some specimens of *C. fornicata* and *C. convexa* were released from their substrata and weighed before the experiment began and re-weighed before being returned to the water to determine the percent wet weight lost. The relationships between the initial wet weight and survival time of the three species were plotted using natural logs and compared using linear regression and analysis of covariance on each pair of species. The sex of the individuals was recorded. Because *C. convexa* remains clamped to the substratum, it is difficult to know precisely when it is dead. Extra specimens were required so that they could be checked for viability on an hourly basis, and included in the calculations if moribund.

To compare *Crepidula convexa* and *C. fornicata* more precisely, animals of the two species were graded into size classes of 100 each by length of shell. Two size classes at a time were set out at 28–30° C, with 30–40% relative humidity. A portion of each size class (10 individuals of 100) was returned to sea water every hour, beginning shortly before the time mortality was expected to occur, based on results from the first experiment. The percent survival was recorded, and the experiment continued, until there were no survivors. Survivorship was indicated by recovery of the animal's ability to cling to a substratum and engage in normal feeding movements, using its gill to create currents and lifting its shell up and down. Survivorship curves were drawn for each size class.

RESULTS

Specimens of *Crepidula fornicata* that were exposed on the beach at low tide gaped much in the manner of *Geukensia demissa*. They lifted the anterior portion of the shell high off the substratum, exposing the mantle cavity. Some specimens raised and lowered the shell repeatedly, while others remained for several minutes in the gaped position. The specimens were in stacks on small stones or bottles that had probably washed ashore with the attached snails. *C. fornicata* and *C. plana* attached to the undersides of *Limulus polyphemus*, when the horseshoe crab was turned over, did not begin gaping immediately. *C. plana* inside empty *Lunatia heros* shells gaped in a manner similar to *C. fornicata*. They too had probably reached the intertidal zone fortuitously.

Specimens of *C. convexa* were found living intertidally on *Littorina littorea*. Of all the species of *Crepidula, C. convexa* is the most mobile and was observed to move from one substratum to another, even as an adult. Adults of *C. plana* and *C. fornicata*, however, were never observed moving in the field. Living specimens of *C. convexa* were observed with dry shells, exposed to the sun, firmly attached to the shells of *Littorina littorea* and to bottles and small stones. They were never observed to gape. When a specimen was forcibly removed from its substratum, a drop of water was seen to come from the mantle cavity.

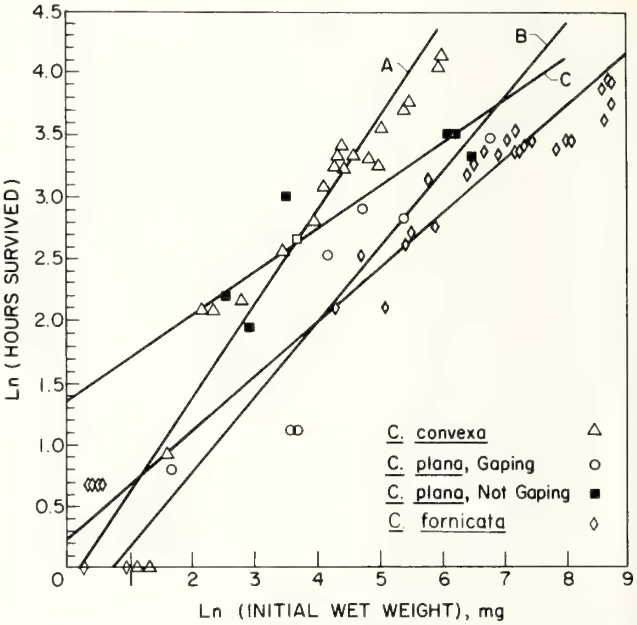

Fig. 1. *Crepidula fornicata, C. convexa* and *C. plana*. Size versus survival time out of water, 22–26° C. The equations for the lines are, using ln functions, *C. fornicata*, Y = .31 + .42x, r^2 = .97 ($p \leq .001$); *C. convexa*, Y = -.24 + .77x, r^2 = .92 ($p \leq .0001$); *C. plana*—gaping, Y = -.58 + .62x, r^2 = .82 ($p \leq .005$); *C. plana*—not gaping, Y = 1.35 + .34x, r^2 = .83 ($p \leq .005$). N = 29 for *C. fornicata*, 21 for *C. convexa*, 7 for *C. plana* gaping, and 6 for *C. plana*, not gaping. The relationship of the log values on the x and y axes to the raw values is: 1 = 2.7; 2 = 7.4; 3 = 20.1; 4 = 54.6; 5 = 148.4; 6 = 403.4; 7 = 1,097; 8 = 2,981; 9 = 8,103.

Crepidula convexa lives in the lower intertidal zone; it was not observed in the splash zone. Neither it nor the other species of *Crepidula* were ever found intertidally on boulders, as true limpets are found. *C. convexa* was also observed in subtidal waters, often on eel grass blades.

Only on one occasion did I observe a specimen of *Crepidula fornicata* to gape while brooding eggs in the field. Twice this phenomenon was observed with *C. plana*.

Preliminary to the experiments, observations of the three species in the laboratory confirmed the differences in behavior seen in the field. After being removed from the water, specimens of *C. fornicata* either raised and lowered the shell almost continuously, or raised the shell and remained in that position with only occasional shell movement until reaching a moribund state. *C. plana* raised its shell also; the larger individuals gaped more than smaller ones. *C. convexa* remained firmly attached to the substratum for as long as six days. Some *C. convexa* were loosened from the substratum after three hours' exposure; they released a drop of water from the mantle cavity. They were unable to regain firm attachment if kept out of water and died within a few hours.

Table 1. *Crepidula convexa* and *Crepidula fornicata*. Percent and rate of weight loss at 22–26° C air temperature. $\bar{x}$ = mean; $S_{\bar{x}}$ = standard error of the mean; N = sample size; M = male, F = female, and I = intermediate (changing sex).

Species	1 Sex	2 Length (mm)	3 Initial Wet Weight (mg)	4 Percent Weight Loss at Death	5 Average Rate of Weight Loss (mg/hr)	6 Average % Weight loss/hr
C. convexa	M	3.4	6.0	40.0	0.69	11.4
(N = 7)	M	5.6	20.7	41.5	2.46	11.9
	M	6.4	25.9	24.3	1.80	6.9
	I	7.7	37.8	28.0	3.03	8.0
	F	8.4	62.7	11.5	2.06	3.3
	F	9.5	96.4	34.0	4.37	4.5
	F	12.4	262.1	28.0	6.39	2.4
				$\bar{x}$ = 29.6		
				$S_{\bar{x}}$ = 3.9		
C. fornicata	M	8.3	55.9	31.7	2.4	4.2
(N = 11)	M	9.6	65.1	24.7	4.6	7.1
	M	9.7	85.0	21.6	2.5	2.9
	M	18.5	593.0	23.9	12.3	2.1
	F	25.8	1,263.8	22.7	25.0	2.0
	F	28.8	1,457.1	31.1	19.7	1.4
	F	29.7	3,205.3	21.4	29.9	0.9
	F	31.5	4,995.9	13.6	34.8	0.7
	F	32.2	4,317.1	22.8	42.8	1.0
	F	32.2	2,352.1	10.8	24.2	1.0
	F	33.0	2,702.2	15.3	21.2	0.8
				$\bar{x}$ = 21.8		
				$S_{\bar{x}}$ = 2.0		

Figure 1 compares the survival times and sizes by initial weight of the three species in air at 22–26° C. A power curve gave the best fit of the data, so the curves were converted to linear regression using the ln function; all regressions were significant. Except for the comparison of *C. convexa—C. plana* gaping, all intercepts were significantly different ($p < .01$ or less). Except for *C. fornicata —C. plana* not gaping, all slopes were significantly different ($p < .05$ or less). Within a species, greater size conferred longer survival. At sizes greater than about 60 mg initial wet weight, survivorship increased in the order *C. fornicata* (gaping) ≤ *C. plana* (gaping) < *C. plana* (not gaping) < *C. convexa*. In animals of the same weight, survivorship was poorest for *C. fornicata*. Survivorship of *C. plana*, gaping and not gaping, converged at about 450 mg. At body size less than 30 mg, there are few data points for *C. plana*, and the reliability of the curves in Figure 1 is in doubt. Despite the few data points for *C. plana*, they are included as preliminary results to provide a hypothesis for future work. Those *C. fornicata* between 1–4 mm in length (wet weight of 1–3 mg) survive less than three hours, while individuals of *C. convexa* in this size range survive up to eight hours. Specimens of *C. plana* attached inside other gastropod shells tended not to gape and survived longer than exposed individuals.

Individuals of *Crepidula fornicata* brooding eggs had higher survivorship than those not brooding. However, the eggs themselves became damaged when the shell was raised. Microscopic examination of the egg masses of three females left out of water for 24 hours showed the breakdown of 40 to 70% of the embryos. The eggs of *Crepidula convexa* suffered few ill effects while being held under the shell of a female out of water. In the laboratory, viable young were released from females that had remained out of water for ten hours at 24° C and for six hours at 30° C air temperature.

Table 1 provides information on the relationship between size, percent weight loss at death, and rate of water loss in *C. fornicata* and *C. convexa*. Within species, there is no clear relationship between length or wet weight (columns 2 and 3) and the percent weight loss at death (column 4) for either species. *C. convexa* tolerated more water loss on average than *C. fornicata* (~ 30% vs. ~ 22% water lost at death). But in similar-size animals, e.g. 8.4 mm *C. convexa* and 8.3 mm *C. fornicata*, the latter had a larger percent weight loss. The rate of water loss (column 5) is slightly larger for small individuals of *C. fornicata* compared with *C. convexa* of similar size although there are ambiguities in the data (the third specimen of *C. fornicata* lost water more slowly than predicted by the data for other specimens). The larger *C. fornicata* lost water at a much faster rate than smaller specimens of either species. However, the rate of water loss as a percentage of the body weight is inversely related to body size, intra- and interspecifically (column 6).

Survivorship curves for different size classes of *Crepidula fornicata* and *C. convexa*, 28–30° C, are presented in

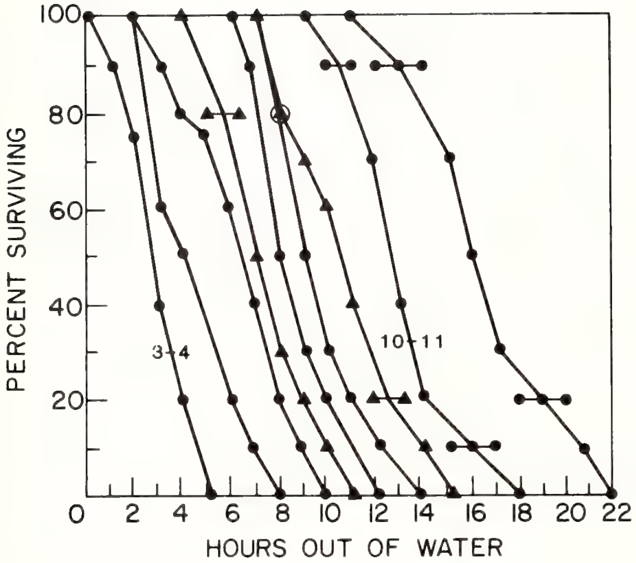

Fig. 2. *Crepidula convexa*. Percent survival versus time out of water; each line represents 100 individuals. A bar connects consecutive hours when no change occurred in the percent surviving. Open circles indicate overlaps of adjacent curves. The nine lines represent nine one-mm shell-length classes, beginning with > 3 to 4 mm on the left and ending with > 11–12 mm on the right.

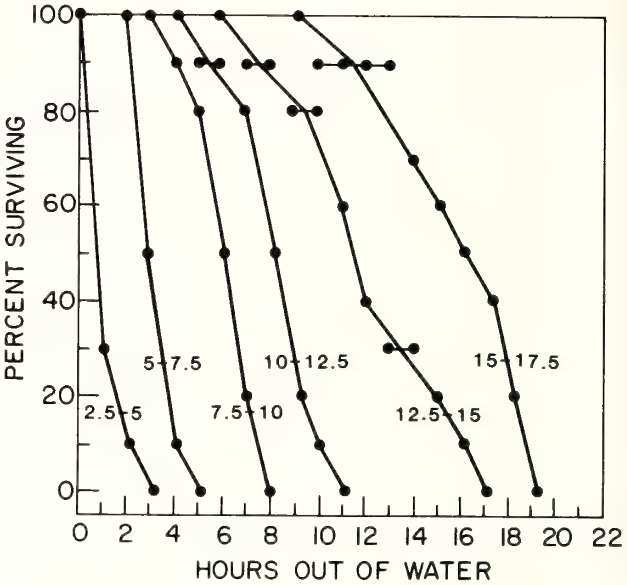

Fig. 3. *Crepidula fornicata*. Percent survival versus time out of water; each line represents 100 individuals. Shell length given in mm. Six 2.5-mm shell-length classes, beginning with > 2.5–5.0 mm on the left and ending with > 15.0–17.5 mm on the right. Notations as in Fig. 2.

Figures 2–5. The steeper decline of the sigmoid curves of smaller individuals of *C. fornicata* and all *C. convexa*, relative to larger *C. fornicata* (Figs. 2–3 vs. 4–5) indicates that most members of each of these size classes die nearly simultaneously. Larger individuals show much greater variability in time of death. In specimens of a given size, *C. convexa* survives longer than *C. fornicata* (Figs. 2–3).

Figures 6 and 7 present the relationship of shell length and time to 50% mortality for *C. convexa* and *C. fornicata*, respectively, at 28–30° C. The lines have been drawn point-to-point. For *C. convexa*, there is a break in the exponential curve at about 6 mm, just at the size when most individuals of *C. convexa* are changing sex. For *C. fornicata*, there is a suggestion of a similar break in the curve. These discontinuities are not removed by plotting the data on log-log paper; the two portions on either side of the discontinuity have significantly different slopes. Sex change occurs over a wider size range in *C. fornicata* and cannot be correlated precisely with the change in slope (Hoagland, 1978) but at 22 mm most of the individuals in this sample were in the process of changing sex.

DISCUSSION

A marine gastropod exposed to air must cope with temperature control and respiration while minimizing water loss. Shell-raising allows direct oxygen exchange and evaporative cooling but increases desiccation. Three sympatric species of *Crepidula* differ in their behavioral responses to aerial exposure, with direct physiological consequences. The difference is best documented between the very small and frequently intertidal *C. convexa* and the largest and least frequently intertidal species, *C. fornicata*. Table 1 suggests that *C. fornicata* is not any more able to tolerate water loss on an equal size basis than *C. convexa* (column 4), yet its gaping behavior increases its rate of water loss, especially in small individuals. Larger individuals of *C. fornicata* are partially protected by their larger mass and lower rate of water loss.

Comparison of laboratory results to field conditions must be made cautiously. The experiments only show the relative responses of the species, not the actual magnitude of desiccation and stress experienced in the field. Survival in the field could be lower than observed in these experiments because some individuals do not recover when returned to the water after having lost the ability to grip the substratum, but before having lost the ability to respond to touch. Also, the animals in these experiments were not exposed to the direct sun. All but the smallest *C. fornicata* survived in the laboratory for as long as they would have been exposed in most intertidal situations, but survival of settling juveniles might be the critical factor in distribution of the species in shallow water. Newell (1976) pointed out that lethal levels of water loss are rarely achieved in one day, but that there can be a cumulative net loss over several days of a low tide cycle. The rate of regaining water can be less than the rate of water loss (Davies, 1969). Mortality also can be caused indirectly in limpet-shaped gastropods, which lose muscular control and are more vulnerable to predation as sublethal levels of desiccation are reached (Verderber *et al.*, 1983).

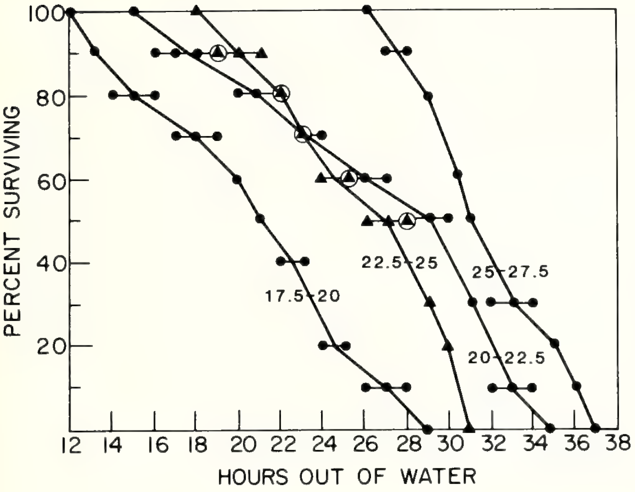

Fig. 4. *Crepidula fornicata.* Percent survival versus time out of water. The four lines represent the shell-length classes > 17.5–20.0 mm on the left to > 25.0–27.5 mm on the right. Continuation of Fig. 3.

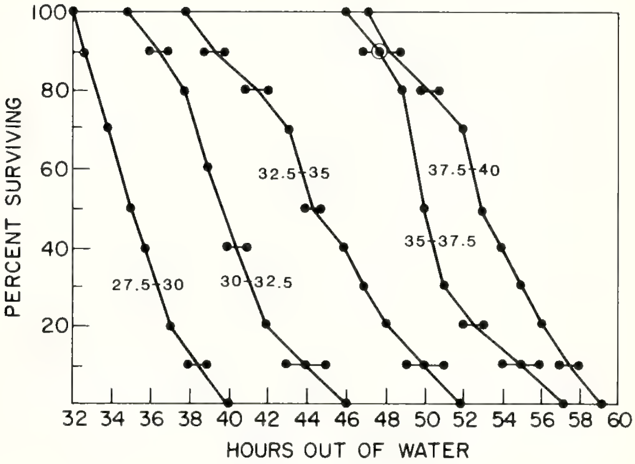

Fig. 5. *Crepidula fornicata.* Percent survival versus time out of water. Five 2.5-mm shell-length classes, > 27.5–30 mm to > 37.5–40.0 mm. Continutation of Fig. 4.

Differences in results of the two laboratory experiments themselves show the importance of temperature, relative humidity, and individual variation, especially in body size. Limited numbers of individuals yielded data for the first experiment, especially in the smaller size categories of all species. The shapes of the curves in Figure 1 are sensitive to the low number of data points in the small size ranges; the second experiment is more reliable in the smaller size categories (length < 10 mm in *C. fornicata*; < 5 mm in *C. convexa*).

Brooded embryos of specimens of *Crepidula fornicata* appear to be damaged during prolonged gaping, whereas damage to broods of aerially exposed *C. convexa* is less likely. More rigorous, longer-term data are required. Pechenik (1978) pointed out that protection of embryos depends upon adult behavior in gastropods; certainly that is true in *Crepidula.*

In remaining clamped to the substratum out of water, *Crepidula convexa* must tolerate accumulated wastes, high temperature, and low oxygen tension. Anaerobic metabolism is found in many mollusks (Trueman and Akberali, 1981; Brinkhoff *et al.*, 1983) and is possible in *C. convexa.* Stress to *Crepidula plana* during aerial exposure is very dependent on its position, whether inside a dead shell, or exposed. *C. plana* is intermediate between *C. convexa* and *C. fornicata* in that only some adults gape when exposed to air. For a given shell length, *C. plana* has a smaller volume and larger foot surface area than the other species (Hoagland, 1977). It may have difficulty when gaping due to its high surface-to-volume ratio.

Similar species of *Crepidula* found along the California coast are ecologically equivalent to the Atlantic species. The large species that releases veliger larvae, *C. onyx*, and the planar species, *C. nummaria*, are rarely intertidal. *C. adunca*, a small direct-developing species, lives intertidally on living gastropods as well as subtidally. It would be of interest to compare the responses of these species to aerial exposure, to see if the pattern seen for the western Atlantic species is general within *Crepidula.*

Crepidula can also be compared with species of marine clams. The horse mussel *Modiolus modiolus* (Linnaeus), a subtidal species, gapes widely when aerially exposed (Bayne, *et al.*, 1976). *Geukensia demissa* [= *Modiolus demissus a* (Dillwyn)], the ribbed mussel, lives high in the intertidal zone. It also gapes, but in a controlled manner that reduces water loss while allowing evaporative cooling (Lent, 1968, 1969). *Mytilus edulis* Linnaeus, like *C. convexa*, inhabits tidepools and lower portions of tidal flats. It retains water in the mantle cavity and is capable of anaerobic metabolism (Coleman and Trueman, 1971). Bayne *et al.* (1976) found that most intertidal *Mytilus californianus* Conrad do not gape in the field, but nonetheless water loss can occur through the pedal gape. In the laboratory, controlled gaping was common only when the relative humidity was high. McMahon (1983) found that the intertidal bivalve *Geloina erosa* periodically opens its inhalent siphon and uses the mantle cavity for aerial respiration, causing water loss, but that the behavior disappears after a time, perhaps due to the need for water conservation. *Cardium edule* also gapes (Widdows *et al.*, 1979). These examples show that a similar variety of responses to aerial exposure occur in bivalves and in *Crepidula.*

In the prosobranch limpets, high intertidal species of Hong Kong tend to keep the shell down when out of water, while species living lower in the tide zone tend to raise the shell, much as I found for Crepidula in New England (Daniel, 1982). Davies (1969), comparing desiccation with the vertical distribution of *Patella aspera* Lamarck and *P. vulgata*, found that the rate of water loss as a percent of the total body

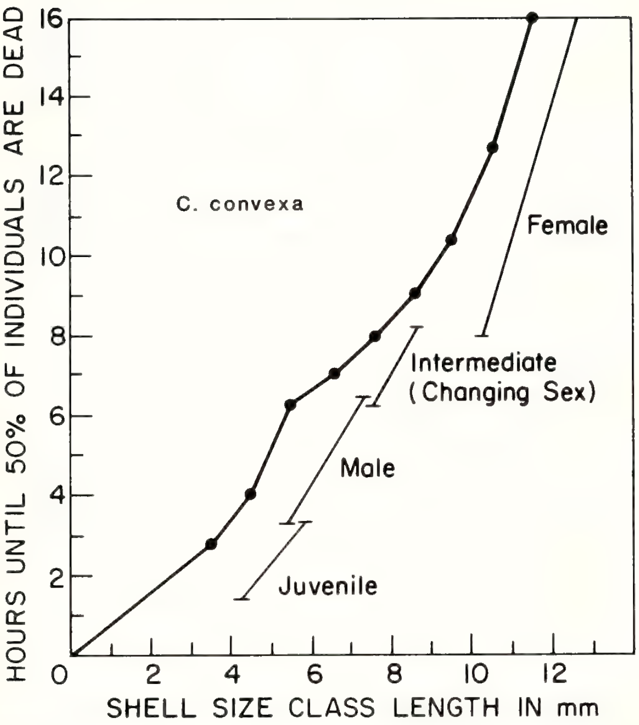

Fig. 6. *Crepidula convexa*. Size class related to desiccation. Values are interpolated from Fig. 2. Curves are fitted by eye.

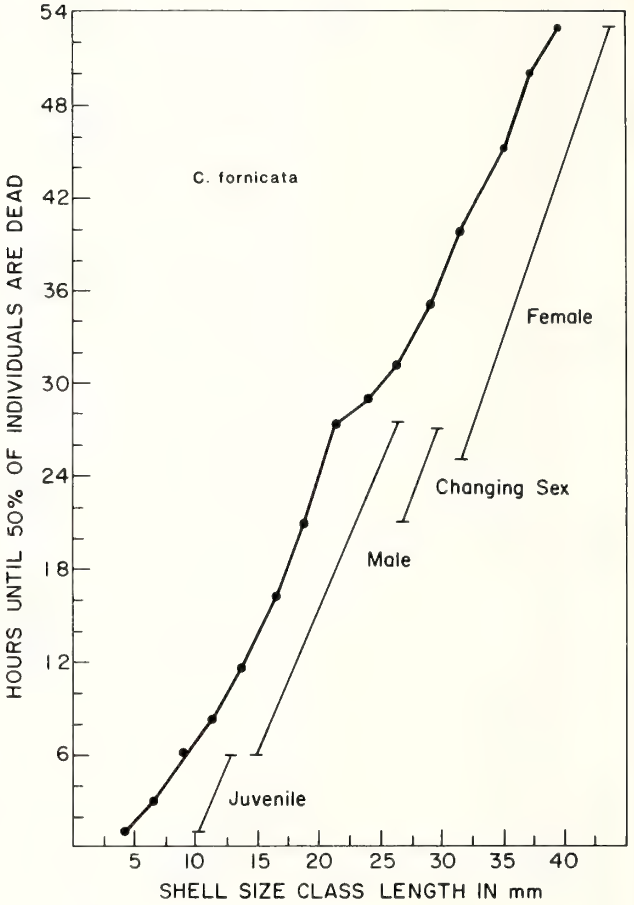

Fig. 7. *Crepidula fornicata*. Size class related to desiccation. Values are interpolated from Figs. 3–5.

weight was inversely proportional to body size, as was shown for *Crepidula* in Table 1. Water loss at 50% mortality of the low intertidal species, *P. aspera*, was 30–35%, whereas water loss at 50% mortality of the higher intertidal *P. vulgata* was 50–65%, depending on the population sampled. Comparable values for *Crepidula* were 22% for *C. fornicata* and 29% for *C. convexa*. Broekhuysen (1940) and Brown (1960) found that low intertidal species succumbed to a lower percent water loss than those living at higher intertidal levels. Kensler (1967) found that specimens of a single species living on an upper shore were more resistant to desiccation than lower-shore specimens. The limited data available therefore suggest a correlation between the time a population is aerially exposed and the percentage of its weight it can lose as evaporation before death ensures. The same pattern is known for hermit crabs (Young, 1978). Also, there is a tendency for subtidal and low intertidal crabs (Ahsanullah and Newell, 1977) and barnacles (Foster, 1971; Barner *et al.*, 1963) to have a higher evaporation rate than high intertidal species. For all species of invertebrates, large size provides protection from desiccation, allowing species like *Crepidula fornicata* the luxury of using evaporative cooling and aerial respiration when exposed to air, compared with *C. convexa*.

Shotwell (1950) and Segal (1956) suggested a positive relationship between size of the water storage space and vertical distribution in limpets. The frequently-intertidal *C. convexa* and *C. adunca* have a proportionately smaller foot and larger mantle cavity than *C. fornicata* and *C. onyx* (Hoagland, 1977). However, in a thorough study of limpet physiological ecology, Wolcott (1973) found that total water stored, including that in the body itself, is a better measure than extrapallial or mantle-cavity space of the ability to withstand desiccation.

Orton (1929, 1932) examined the height of limpets living along a gradient of aerial exposure. More highly peaked shells of *Patella vulgata* Linnaeus were in the more desiccating environments, but no such relationship was established for two species of *Acmaea*. *Crepidula convexa* and *C. adunca* in the intertidal zone are more peaked than those living subtidally, but this is because they grow in conformity to the substratum—the highly convex surfaces of other living gastropods, e.g., *Littorina littorea* (Linnaeus). For *C. fornicata*, substrata in the intertidal zone and hence the snails themselves are usually flatter than in subtidal situations, where the animals form stacks and are highly arched. Multiple environmental pressures act on such features as shell height and size, and correlation of shell height with one environmental factor such as desiccation is unwarranted.

CONCLUSIONS

The sympatric species of *Crepidula* in the Northwestern Atlantic differ in response to aerial exposure, although the mechanisms behind the behavioral differences have not been identified. Nevertheless, there is a pattern in these differences. *Crepidula convexa* is more frequently in the intertidal zone, and for a given size animal, appears more able to withstand aerial exposure. *C. plana* avoids desiccation by choice of substratum, such as the inside of a dead gastropod shell occupied by a hermit crab. Small specimens of *C. fornicata* are highly susceptible to desiccation. While species differences in behavior correspond to differences in habitat preferences, this work does not prove that aerial exposure is the factor directly controlling zonation of *Crepidula*. Other mollusks also show intra-generic differences in adaptation to aerial exposure, which correspond to habitat preferences and behavioral patterns, e.g., gaping in low-intertidal mollusks and closing behavior in higher-intertidal species; similar patterns exist in crustaceans.

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THE NAIAD FAUNA OF THE TELLICO RIVER, MONROE COUNTY, TENNESSEE

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ABSTRACT

The Tellico River, approximately 90 km in length, is the major tributary of the Little Tennessee River in East Tennessee and supports a freshwater mussel population comprised of 15 species. Limited archaeological evidence indicates that an additional eight species inhabited the lower reaches of the river 200 years ago. Species diversity and numbers are greatest in the stretch of river between TRM 21.5 (34.4 km) and TRM 22.5 (36.0 km), the most suitable habitat occurring at Nars Ford (TRM 21.5–22.0: 34.4–35.2 km) which has a substrate of cobbles, gravel and sand. The composition and relative abundance of the Tellico River mussel assemblage are presented; prior to this study only limited collections of mollusks had been made and published references to Tellico River naiads are few. Although the Nars Ford mussel population appears viable, its restriction to about 1 km of the river makes it highly vulnerable to destruction by silting and pollution.

The Tellico River originates from the junction of Bob Creek, Round Mountain Branch and two other small unnamed creeks in Cherokee County, North Carolina and flows west and north for 90 km to its confluence with the Little Tennessee River, Monroe County, Tennessee (Fig. 1). Over a period of 56 years (1926–1981), the average discharge gaged at the city of Tellico Plains at Tellico River Mile (TRM) 27.5 (44.0 km) was 284 ft^3/s. Water temperature may vary from 0.5°C in December–January to 25.0°C in July–August. The substratum of the Tellico River from its origin to within about 3 km of Tellico Plains consists of flat bedrock, boulders, and large cobbles with only small and isolated areas of gravel and sand that could serve as suitable habitat for the establishment of mussels.

Although numerous coarse sand and gravel bars occur from Tellico Plains downstream to the beginning of impoundment at about TRM 19.0 (30.4 km), heavy siltation is evident over long intermittent stretches of this section of the river. On November 29, 1979 the Tennessee Valley Authority shut the gates on the newly constructed Tellico Dam, thus transforming the Little Tennessee River into Tellico Lake and, in the process, impounding the lower 30 km of the Tellico River. The diversity and extent of preimpoundment mussel populations in this stretch of the river are unknown. The only species reported by Ortmann (1918) from the Tellico River, Monroe County (exact location unknown) were *Fusconaia barnesiana* (Lea, 1835) and *F. barnesiana bigbyensis* (Lea, 1841). Both the Paper Pond-shell, *Anodonta imbecilis* (Say, 1829) and the Common Floater, *Anodonta grandis grandis* (Say, 1829) have become well established in the impounded lower section of the Tellico River, apparently as a result of reduced water flow, heavy siltation and establishment of a lake-like habitat. Neither species were encountered in the unimpounded stretches of the river during this study.

METHODS

During an ichthyology field trip to the Tellico River in March 1981, aquatic biology students in the Department of Zoology, University of Tennessee, Knoxville, collected a few naiad shells and brought them to one of us (Parmalee) for identification. A few additional specimens were obtained by other students and us on subsequent field trips to the river in 1982, but it was not until 1983 that efforts to make a systematic collection of the Tellico River to determine the location and extent of freshwater mussel populations was initiated.

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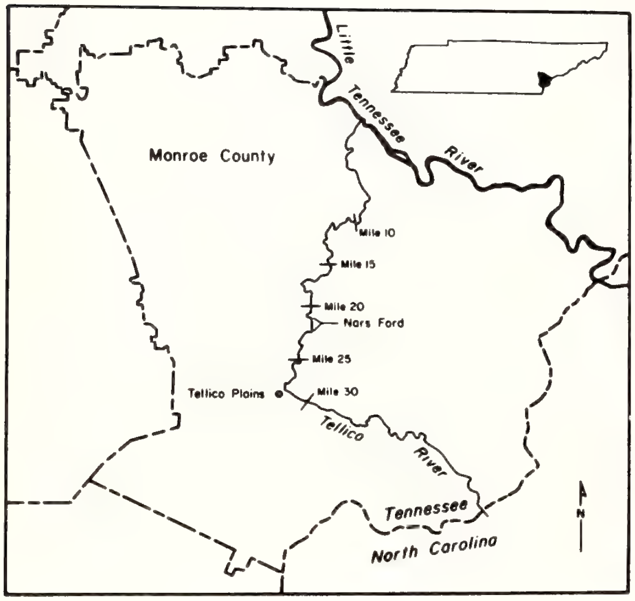

Fig. 1. Tellico River, Monroe County, Tennessee and location of Nars Ford and river miles surveyed (TRM 13.5–30.0: 21.6–48.0 km).

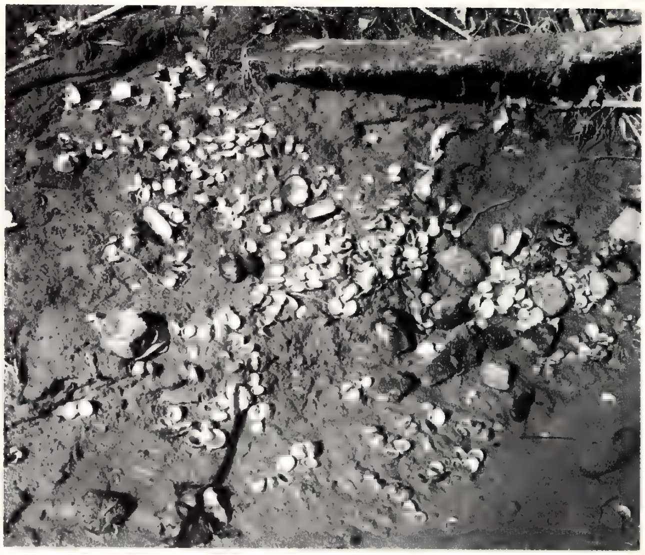

Fig. 2. Typical winter muskrat shell midden at Nars Ford, Tellico River.

Four locations above Tellico Plains to about TRM 30.0 (48.0 km) were examined in 1982 but neither living individuals nor old shells of any species of bivalve (including the Asiatic Clam, *Corbicula fluminea* (Müller, 1774)) were noted. Reliable observers who consistently fish the upper stretches of the Tellico River for trout report that no shells in these sections have ever been seen.

It became apparent that any viable freshwater mussel populations in the Tellico River probably occurred below Tellico Plains to at least the area of impoundment. This section of the river was surveyed by boat and by wading the shallow sections, the majority of specimens being obtained from midden piles that accumulated as a result of foraging activities by raccoons, mink and muskrats. However, it is believed that, on the basis of gnawed marks on valves and the method of "stockpiling" shells (Fig. 2), most accumulations reflect muskrat feeding activitity. Specimens were returned to the Frank H. McClung Museum, University of Tennessee for cleaning, accessioning and incorporation into the research and reference mollusk collection. Voucher specimens of most species represented in our Tellico River collections were sent to the Museum of Zoology, The Ohio State University, Columbus and to the Department of Malacology, the Academy of Natural Sciences of Philadelphia.

Five collecting trips were made in 1983 (January 30, February 19, September 1, November 15 and 26) and two in 1984 (February 22, March 15). Predation on mussels by muskrats appears to intensify in the fall (about October) and this food resource is heavily exploited throughout the winter until spring (about April) when it tapers off. Our largest samples of fresh shells were obtained in November, December, January and February. Table 1 represents a compilation of specimens collected on four trips taken during these months in a stretch of the Tellico River (TRM 21.5–22.5: 34.4–36.0 km) that supports the only remaining large mussel populations.

RESULTS AND DISCUSSION

Nars Ford (TRM 21.5–22.2: 34.4–35.5 km) is characterized by a swift current, a normal river stage depth of .3-1 m, and a substratum composed of small cobbles, gravel and sand. It is within this single short stretch of the Tellico River that the greatest species diversity and numbers of freshwater mussels occur (Fig. 3). During a float trip on November 26, 1983 from TRM 28.0 (44.8 km) to Nars Ford, the first shells encountered (*Villosa vanuxemensis* (Lea, 1838) and *Pleurobema oviforme* (Conrad, 1834)) were found at approximately TRM 25.0 (40.0 km). It was at about this point that the first specimens of *C. fluminea* were also found. Naiads did not become numerous until TRM 22.5 (36.0 km). Exclusive of an abundant *C. fluminea*, less than a dozen shells of recently eaten mussels were recovered in muskrat middens during a float trip February 22, 1984 between TRM 21.5 (34.4 km), the lower end of Nars Ford, and TRM 19.5 (31.2 km).

The effects of impoundment—a gradual widening of the river, mud covered banks and adjacent flats, dead trees bordering the main channel, and water level marks distinguishing summer high pool and winter draw down—become apparent at about TRM 19.0 (30.4 km) and pro-

Table 1. Species and number of freshwater mussels found at Tellico River Mile 21.5–22.5 (34.4–36.0 km) during four winter collection trips, 1983–1984.

Species	No. of Specimens	%	Fauna*
Fusconaia barnesiana (Lea, 1838)	103	9.16	C
Fusconaia subrotunda (Lea, 1831)	44	3.91	C
Elliptio crassidens (Lamarck, 1819)	5	.44	U
Elliptio dilatata (Rafinesque, 1820)	2	.18	U
Pleurobema oviforme (Conrad, 1834)	99	8.80	C
Strophitus undulatus (Say, 1817)	2	.18	U
Toxolasma lividus (Rafinesque, 1831)	20	1.78	C
Lampsilis fasciola (Rafinesque, 1820)	49	4.36	U
Lampsilis ovata (Say, 1817)	8	.71	U
Medionidus conradicus (Lea, 1834)	18	1.60	C
Potamilus alatus (Say, 1817)	5	.44	U
Villosa iris (Lea, 1829)	227	20.18	C?
Villosa vanuxemensis (Lea, 1838)	543	48.27	C
Totals	1125	100.01	

* C-Cumberlandian
U-Undetermined

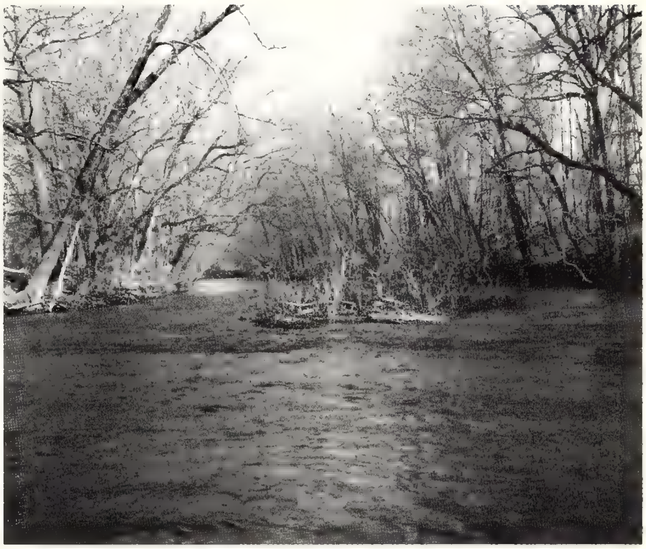

Fig. 3. Riffle area in Nars Ford, Tellico River.

nounced by TRM 17.0 (27.2 km) (Fig. 4). Of interest is the fact that muskrat shell middens, from TRM 18.5 (29.6 km) to TRM 14.5 (23.2 km), occurred at full pool level (813 feet MSL). This level was maintained for the remaining 1979–1980 winter period and during the summer of 1980. It was apparently during this period that muskrats exploited the naiad populations in the newly impounded stretches probably for the last time as the former shallow riffles and shoals were now deeply submerged and the substrate was becoming silted over. When shells of endemic species (exclusive of *Anodonta* spp.) were present, they and *C. fluminea* were chalky and the middens were usually partly covered with sand and debris. No fresh (1983) specimens of species characteristic of the Nars Ford assemblage were encountered in the impounded stretches of the Tellico River surveyed (TRM 19.5–13.5: 31.2–21.6 km) during this study. However, piles of fresh *C. fluminea* were noted along the banks and on rock ledges, indicating their presence in the river and recent use by muskrats. It appears that, based on the chalky, eroded condition of the valves in the old middens and the lack of fresh specimens in association with *C. fluminea* in recent muskrat accumulations, all endemic species other than *Anodonta* spp. were eliminated from the impounded stretches of the Tellico River by the end of 1980 or during 1981.

Based on the data presented in Table 1 summarizing the four largest winter collections from Nars Ford, individuals of *Villosa vanuxemensis* comprise approximately half of the entire endemic mussel population. Next in abundance was *V. iris* (Lea, 1829), accounting for 20% of the total. Specimens of *Fusconaia barnesiana* (Lea, 1838) and *Pleurobema oviforme* each represented about 9% of the population, thus these four species comprised 86% of the individuals from this stretch of the Tellico River. We recognize a possible bias (underrepresentation) in the case of large specimens of species such as *Lampsilis ovata* (Say, 1817) and *Potamilus alatus* (Say, 1817) that would be unmanageable by muskrats. Although mature individuals of both species were observed living in the substrate and a few scattered empty shells were encountered, no juvenile specimens of either were found in the muskrat middens. *Lampsilis ovata* apparently only occurs immediately upstream from Nars Ford in substrate composed of greater quantities of fine sand. The same seems to hold true for *Strophitus undulatus* (Say, 1817), although only three specimens have been found thus far. Although no quantitative studies were made of specimens of species represented in individual muskrat middens, it was obvious that shells of *C. fluminea* far outnumbered those of endemic species wherever both were encountered (e.g., see Fig. 2).

Ortmann (1924, 1925) suggested that the distribution patterns of freshwater mussels in eastern North America could be recognized on the basis of geographic location and could be separated into three major groupings: (1) A widely distributed fauna characteristic of the Mississippi and lower Ohio River systems (Interior Basin); (2) species restricted to the Ohio River proper and its major tributaries; and (3), a fauna endemic to the middle and upper Tennessee and Cumberland rivers and their tributaries flowing out of the southern Appalachians and Cumberland Plateau. These "Cumberlandian" species or forms are generally dominant in mussel assemblages inhabiting the streams and rivers of East Tennessee (e.g., the Little South Fork Cumberland River, Starnes and Bogan, 1982; upper Clinch River, Stans-

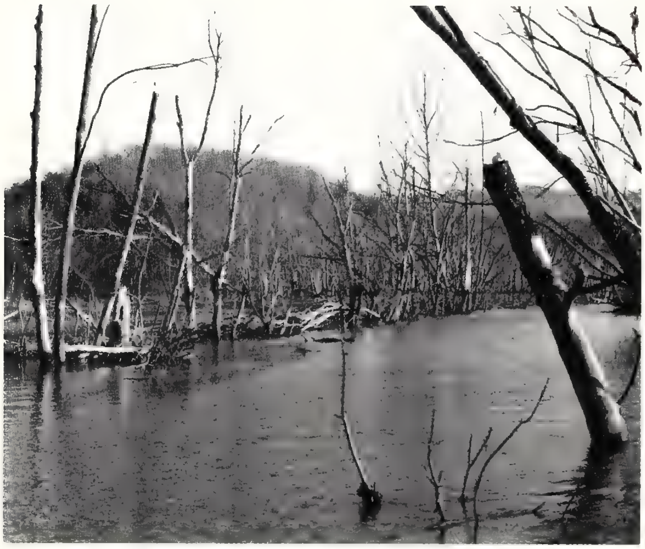

Fig. 4. Lower impounded stretch (about TRM 15.5: 24.8 km) of the Tellico River.

bery, 1973). Approximately half of the species found living in the Tellico River can be referred to as Cumberlandian (Table 1), several of which occur in abundance. The other half, their origins or primary regional affinity either unknown or more closely associated with the Mississippi River drainage, are maintaining numerically low populations. This is assuming that *V. iris* is Cumberlandian in origin (listed by Ortmann [1925] as *Microyma nebulosa* (Conrad, 1834) which he regarded as a Cumberlandian type), but the taxonomy of the *V. iris* complex is unclear and consequently the origin of this group remains uncertain. Nevertheless, at least six species or forms recorded from the Tellico River may be considered Cumberlandian in origin and, with but few exceptions, the species assemblage is typical of similar streams comprising the upper Tennessee River drainage.

Individuals of the six species of uncertain or undetermined origins inhabiting unimpounded stretches of the Tellico River comprised slightly over 6% of the 1125 specimen sample recorded in Table 1. Of these six, *Lampsilis fasciola* (Rafinesque, 1820), a species widely distributed and often abundant in the streams of East and Middle Tennessee, accounted for approximately 4.5% of the total. The rarity of *Elliptio dilatata* (Rafinesque, 1820) (three fresh specimens, one relic) in the unimpounded Tellico River is surprising, considering the fact that once established it often becomes extremely abundant as it has in streams of the upper Tennessee River drainage such as the unimpounded reaches of the Clinch and Powell rivers. However, its occurrence in old (1980–1981?) muskrat middens in some now impounded stretches of the river at about TRM 18.5–13.5 (29.6–21.6 km) suggests that this species may have been more numerous in the lower 30 km than in the Nars Ford area. *Elliptio crassidens* (Lamarck, 1819), a species most often found inhabiting large rivers at depths of about 3–6 m, occasionally appears in small streams but seldom in large numbers. Five specimens obtained in middens at Nars Ford had a mean length of 76.8 cm, height of 53.4 cm and a mean width (greatest thickness of paired valves) of 29.4 cm; all five were very similar in size.

Of the remaining Cumberlandian species inhabiting the Tellico River, *Medionidus conradicus* (Lea, 1834) and *Toxolasma lividus* (Rafinesque, 1831) appear to be the rarest with individuals of each numbering less than 2% of the total. Specimens of *T. lividus* from the Tellico River possess a dark purple nacre and a blackish periostracum. An apparently viable population of *Fusconaia subrotunda* (Lea, 1831) was found at Nars Ford, but individuals comprise only a small part (about 4%) of the total species assemblage. Specimens are only moderately inflated and appear to represent the form *F. s. lesueriana* (Lea, 1840); most individuals are small, the largest collected measured only 75 mm in length.

Fusconaia barnesiana, the one species from the Tellico River reported in the literature (Ortmann, 1918), is described by Ortmann (1918:536) as ". . . very variable in size, shape, color, and sometimes it is hard to distinguish it [the shells] from *Pleurobema oviforme argenteum*." Specimens from the Tellico River are typical of the form *F. b. bigbyensis*; mature individuals may reach a length of 65 mm, but specimens attaining this size are old and exhibit extensive and deep erosion over the anterior two-thirds of the valves. The same condition exists in old individuals of several other species, but especially in *F. subrotunda* and *P. oviforme*. Most specimens of *P, oviforme* from the Tellico River exhibit moderately inflated shells that are similar to those described by Ortmann (1918) from the Little Tennessee River; they are not the compressed form *P. o. argenteum* typical of headwaters and small streams. Both *F. barnesiana* and *P. oviforme* appear to have well established and viable populations in the Nars Ford section of the river and, combined, individuals of these two Cumberlandian species comprise nearly 20% of the naiad assemblage.

During archaeological investigations in the proposed Tellico Reservoir, only one aboriginal site adjacent to the lower Tellico River (TRM 5.0: 8.0 km) containing faunal remains was encountered. Known as the Starnes Site (40MR32), it was composed of five Cherokee farmsteads that had been occupied from about the early 1780s to 1800. Although less than two weeks were devoted to surface collecting and testing, it was felt that most of the refuse pits and other features containing artifacts were located and excavated (Salo 1969). Although the quanitity of shell recovered was small, it is significant because it provides the only documentation of an early naiad fauna in the lower Tellico River and increases the known mussel assemblage by eight species (Table 2). Of interest is the fact that both typical small river or shoal species such as *M. conradicus* (Lea, 1834) *Quadrula intermedia* (Conrad, 1836), *Quadrula sparsa* (Lea, 1841), and *Epioblasma haysiana* (Lea, 1834) and large river species (e.g., *Pleurobema obliquum* (Lamarck, 1819), *Dromus dromas* (Lea, 1834)) occurred together in this aboriginal assemblage. Based on these limited data, it appears that the lower Tellico River about 200 years ago consisted of shoals and extended deeper stretches that provided habitat for a diversified mussel fauna.

Although long stretches of the Tellico River are now bordered by thick stands of brush and timber on banks and hillsides, intermittent and more level flood plain areas have been converted into pasture and cropland. Erosion of cultivated fields has produced silting and a resulting river substratum unfavorable for establishing or maintaining viable mussel populations. Impoundment of approximately the lower 30 km of the river has also produced a habitat unsuitable for most mussels except *Anodonta* spp. and an occasional individual of species more generalized in habitat requirements. Nars Ford and the adjacent short upstream stretch of the river (TRM 21.5–22.5: 34.4–36.0 km) comprise the one remaining area that still supports a varied and abundant naiad fauna characteristic of many upper Tennessee River drainage streams. Without detailed studies of the extant ichthyofauna, extent and depth of pools and silted stretches, variations in rates of flow, effects of periodic flooding, disturbances by cattle when entering the river to drink, predation by muskrats, and other possibly related factors, the reason(s) for a reduced or absent mussel fauna in stretches of seemingly suitable habitat in the Tellico River cannot be adequately determined.

Table 2. Species and number of freshwater mussels recovered at the historic Cherokee Starnes site, Tellico River Mile 5.0 (8.0 km).

Species	No. of Specimens	Fauna*
Fusconaia barnesiana (Lea, 1838)	1	C
Fusconaia subrotunda (Lea, 1831)	9	C
Quadrula intermedia (Conrad, 1836)	1	C
Quadrula sparsa (Lea, 1841)	1	C
Elliptio dilatata (Rafinesque, 1820)	4	U
Lexingtonia dolabelloides (Lea, 1840)	1	C
Pleurobema obliquum (Lamarck, 1819)	3	U
Pleurobema oviforme (Conrad, 1834)	1	C
Actinonaias ligamentina (Lamarck, 1819)	2	U
Epioblasma haysiana (Lea, 1834)	1	C
Medionidus conradicus (Lea, 1834)	1	C
Dromus dromas (Lea, 1834)	8	C
Ptychobranchus subtentum (Say, 1825)	1	C
Villosa iris (Lea, 1829)	1	C?

* C-Cumberlandian
U-Undetermined

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THE LONGITUDINAL DISTRIBUTION OF THE FRESHWATER MUSSELS (UNIONIDAE) OF KINNICONICK CREEK, NORTHEASTERN KENTUCKY

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ABSTRACT

Kinniconick Creek, a sixth-order high quality stream in northeastern Kentucky, yielded 19 native and one introduced species of freshwater bivalves during a recent survey. Longitudinal distribution analysis indicated general agreement with patterns observed for fish and other invertebrates with an increase in the average number of species from 0.5 in the headwaters to 17 in the middle reaches; however, an abrupt decrease to 2.5 was noted at the lowermost stations. Species commonly encountered in descending order of frequency were: *Lampsilis radiata luteola, Ptychobranchus fasciolaris, Fusconaia flava, Corbicula fluminea, Elliptio dilatata, Epioblasma triquetra,* and *Lampsilis ventricosa*. Species judged as rare or of limited distribution were: *Elliptio crassidens crassidens, Anodonta grandis grandis, Lampsilis fasciola, Leptodea fragilis, Quadrula pustulosa pustulosa,* and *Simpsonaias ambigua*. Calculation of faunal resemblance indices for Kinniconick Creek and seven other similar-sized Ohio River valley streams indicated the strongest resemblance with direct middle and upper Ohio River tributaries and the weakest resemblance to a Cumberland River tributary of the lower Ohio valley. The diverse pelecypod fauna of Kinniconick Creek is regarded as exemplary of undisturbed small to medium-sized watersheds in the middle Ohio River; however, the integrity of the fauna is threatened by potential extraction of oil-shale deposits from the watershed.

During an inventory of Kentucky's highest quality aquatic systems (Hannan et al., 1982), Kinniconick Creek in northeastern Kentucky was examined for the presence of freshwater bivalves (Fig. 1). Interest in the mussel fauna of small to medium-sized streams within the middle and upper Ohio River valley has increased in recent years as exemplified by surveys in Indiana, Kentucky, and West Virginia (Houp, 1980; Taylor, 1980a, b, 1981, 1982; Taylor and Spurlock, 1981). This interest stems from growing concern over documenting distributions of rare naiad species within various Ohio River valley states (Stansbery, 1971; Branson et al., 1981), identification of naiad refugia for reinvasion of perturbated rivers and streams (Taylor, 1980a, 1981; Hannan et al., 1982), and the recognition by aquatic biologists and water regulatory agencies of the value of bivalves in documenting changes in ambient water quality associated with stream pollution (Stansbery, 1969; Starrett, 1971; Blankenship and Crockett, 1972; Taylor, 1980c). Relatively undisturbed streams such as Kinniconick Creek are of particular interest and value since they can serve as baseline lotic systems with which others are compared.

The primary purpose of this study was to document the naiad fauna of Kinniconick Creek, describe observed distributional patterns, and compare the fauna of Kinniconick Creek with that of other similar-sized Ohio River valley streams.

METHODS

Study design followed recommendations set forth by Stansbery (1981, pers. comm., i.e., collect 1–3 hr/station with stations 1.6–4.8 km apart situated from headwaters to mouth) to insure as complete coverage of the fauna as possible. Fifteen stations on the mainstem of Kinniconick Creek were surveyed for mussels on 14 July and 14–15 September, 1982 (Fig. 1, Table 1). Tributary streams were primarily dry and thus were not surveyed. Live mussels,

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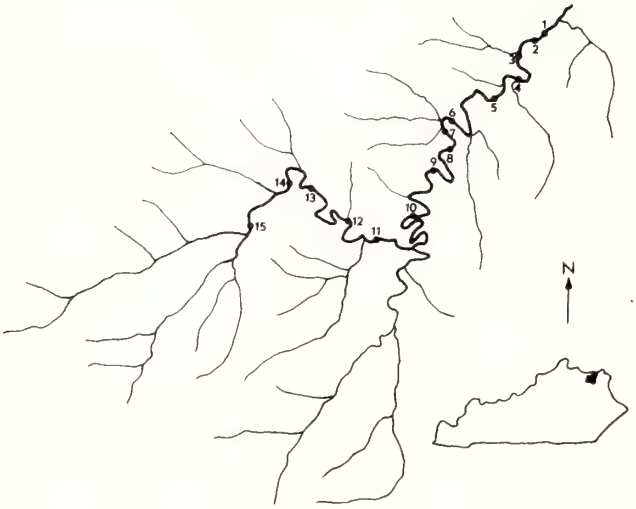

Fig. 1 Sampling stations on the mainstem of Kinniconick Creek, northeastern Kentucky.

along with fresh dead and/or relic shells, were handpicked from shallow water at each station. Shells were also collected from the shoreline, until further searching revealed no additional new species. An average of 2.6 man-hours (0.45–6.00) was spent searching at each station. All specimens were deposited at the Ohio State University Museum of Zoology. Geology, station locations, stream order, and gradients were determined from current United States Geological Survey 7.5 minute topographic and geologic quadrangle maps. Nomenclature follows Stansbery (1982). To estimate resemblance of faunas between two streams, Long's (1963) average resemblance formula was used as follows:

$$C(N_1 + N_2)(100)/2N_1N_2 = \text{average resemblance index (percentages)}$$

C = number of forms common to both faunas
N_1 = number of forms common to smaller fauna
N_2 = number of forms common to larger fauna

Average resemblance index values range from 0 to 100, where 0 indicates that the two faunas have no forms in common, and 100 indicates that the two faunas are identical.

STUDY AREA

Kinniconick Creek is a sixth-order stream arising in Lewis County, Kentucky, at approximately 335 m above mean sea level and flowing 82 km before debouching into the Ohio River at river kilometer 592 at an altitude of 148 m. Average stream gradient from headwaters to mouth is 2.3 m/km. At the time of sampling, the mainstem from stations 1–10 was characterized by long, deep (1.6 m), clear pools

Table 1. Longitudinal distribution of species by station in Kinniconick Creek, Kentucky (L = live specimen, FD = fresh dead specimen, WD = weathered dry specimen, F = fragment).

	1	2	3	4
Leptodea fragilis (Rafinesque, 1820)	WD			
Corbicula fluminea (Müller, 1774)	L	L	L	L
Simpsonaias ambigua (Say, 1825)	FD			
Epioblasma triquetra (Rafinesque, 1820)		WD		
Lampsilis fasciola Rafinesque, 1820			L	
Elliptio dilatata (Rafinesque, 1820)			L	
Ptychobranchus fasciolaris (Rafinesque, 1820)			L	
Lampsilis ventricosa (Barnes, 1823)			L	
Lampsilis radiata luteola (Lamarck, 1819)			L	
Villosa lienosa (Conrad, 1834)			L	
Fusconaia flava (Rafinesque, 1820)			WD	
Elliptio crassidens crassidens (Lamarck, 1819)				
Lasmigona costata (Rafinesque, 1820)				
Quadrula pustulosa pustulosa (Lea, 1831)				
Potamilus alatus (Say, 1817)				
Amblema plicata plicata (Say, 1817)				
Villosa iris iris (Lea, 1829)				
Strophitus undulatus undulatus (Say, 1817)				
Tritogonia verrucosa (Rafinesque, 1820)				
Anodonta grandis grandis (Say, 1829)				
Location (km from mouth)	3.1	3.2	5.8	8.6
Gradient (m/km)	0.86	0.86	1.31	1.31
Total Species/Station	3	2	8	1

Total Species = 20

alternating with short, shallow (7.5–30 cm) riffles of slow to moderate current underlain by gravel and cobble with scattered boulders. Near station 11 a sharp increase in gradient was noted (Fig. 2) and the large pools in this area were separated by long, steep riffles predominated by large cobble, boulder, and bedrock. Field observations indicated that tributaries and the headwaters (above station 15) of Kinniconick Creek were dry or reduced to shallow isolated pools at the time of the survey.

The Kinniconick drainage lies immediately to the west of Pennsylvanian age caprocks defining the edge of the non-glaciated Allegheny Plateau. Quarterman and Powell (1978) described the region as the Northeastern Blue Grass Subsection of the Blue Grass Section of the Interior Low Plateaus Province. The majority of this subsection is within the Kinniconick Creek drainage. Vegetation in the watershed is 90–95% second-growth forest with agricultural development (pasture and row-crops) limited to the generally narrow floodplain. The potential natural vegetation is classified as mixed mesophytic forest (Kuchler, 1964) and is similar to adjacent areas in the non-glaciated Allegheny Plateau. Ridgetops in the watershed are capped by Mississippian age siltstone and shale. Valley slopes are predominantly Mississippian age sandstone, which forms large slump blocks, prominent ledges, and bluffs in parts of the drainage, and to a lesser extent, thin alternating layers of shale and siltstone. Along Kinniconick Creek proper, outcrops of Devonian age Ohio shale or "oil shale" are exposed. The floodplain is composed of Quaternary age alluvium, much of which is derived from tributaries. Substrate particle sizes range from boulder to silty sand, but pebble and cobble, composed of carbonate rocks, siltstone, sandstone, silty shale, and chert predominate. In several areas the creek has cut through the alluvium to expose bedrock. Tributary streams such as McDowell Creek and Laurel Fork are used as sources of gravel for surfacing secondary roads as evidenced by bulldozing in these stream beds during fieldwork.

RESULTS

Collection efforts in Kinniconick Creek yielded 19 native and one introduced species (*Corbicula fluminea*) of freshwater bivalves (Table 1). Shells were generally in good to excellent condition showing little sign of umbo or periostracum erosion. The bulk of the collections was comprised of live specimens; relic or fresh dead shells were scarce both in and along the stream.

For comparative purposes the average number of species was determined for nine segments (stations 1–2, 3–4, 5, 6–8, 9–10, 11, 12, 13, and 14–15, respectively) of the stream having different calculated gradients (Fig. 2). The number of species present in segments represented by a single station was considered an average for that segment.

(Table 1, continued.)

5	6	7	8	9	10	11	12	13	14	15
L										
L	WD									
		L								
L		L	L	WD	L					
L										
L		L	L	WD	L					
L	F	L	L	L	WD					
L		L	L	L		L				
L		L	L	L	L	L	L			
L			FD				L			
L		L	L	WD	L					F
L										
L			L							
L			FD							
L			FD	L						
L		WD	L		FD					
L		WD			FD					
L		L	L		L		L			
		L	L	L	L					
						L	L			
11.9	19.1	20.4	22.5	25.1	29.8	41.3	45.6	50.3	55.0	60.0
0.69	1.35	1.35	1.35	0.80	0.80	1.43	1.42	3.14	0.91	0.91
17	2	11	13	8	9	3	4	0	0	1

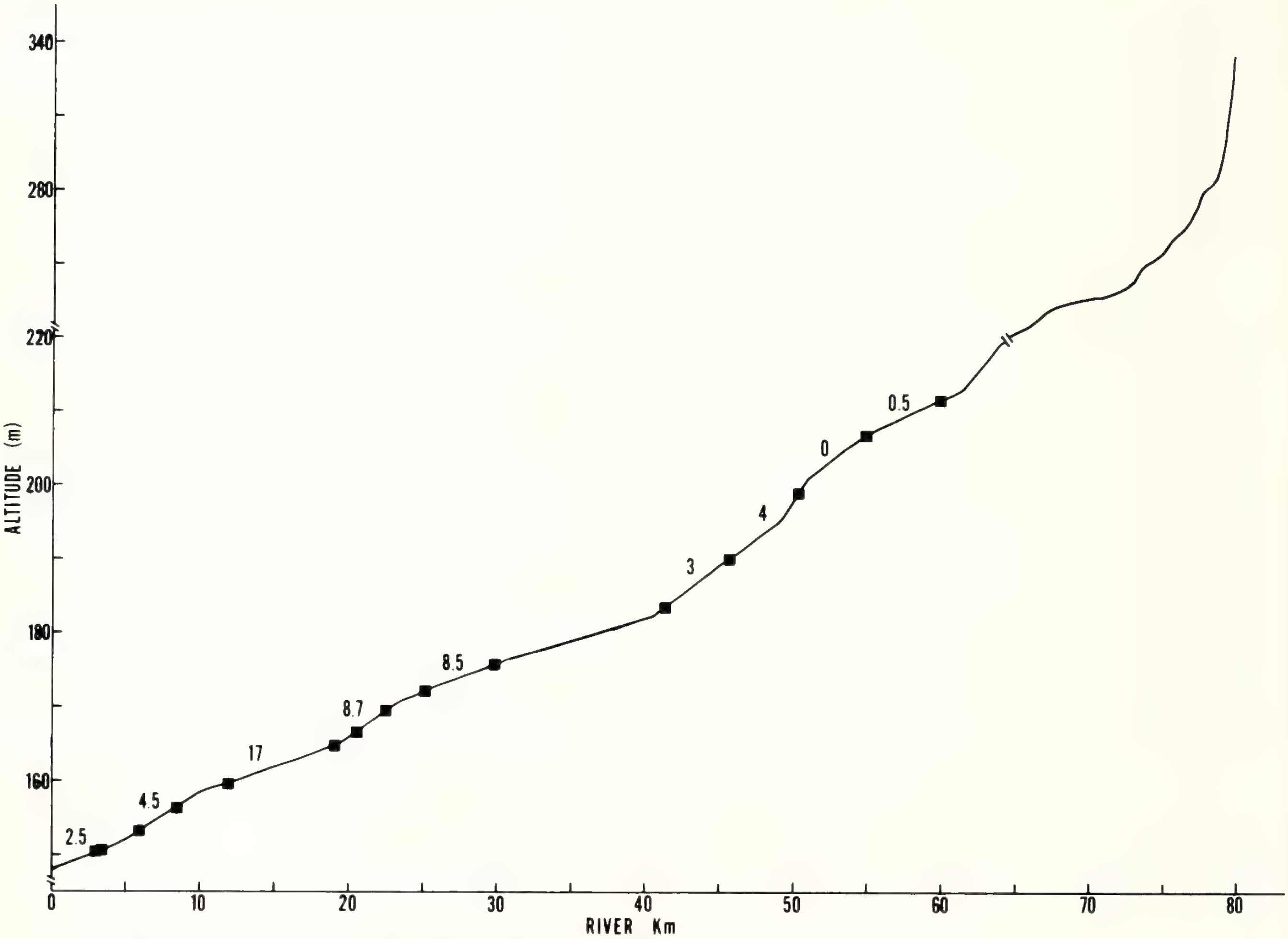

Fig. 2 Average number of species from segments of different calculated gradients in relation to altitudinal changes in Kinniconick Creek mainstem. (Collecting stations are denoted by solid squares).

The average number of species per segment increased from 0.5 (stations 14–15) in the headwaters to 17 in the middle reaches (station 5) and decreased abruptly near the mouth to 2.5 (stations 1–2). Rank correlation ($r = -0.52$) between gradient and average number of species per segment was not significant ($P < 0.5$).

The most commonly encountered species (40% or more stations) in descending order of importance were: *Lampsilis radiata luteola* (53%), *Fusconaia flava* (47%), *Ptychobranchus fasciolaris* (47%), *Corbicula fluminea* (40%), *Elliptio dilatata* (40%), *Epioblasma triquetra* (40%), and *Lampsilis ventricosa* (40%). Species judged as rare or of limited distribution (less than 15% of the stations) within the drainage were: *Anodonta grandis grandis* (13%), *Lampsilis fasciola* (13%), *Leptodea fragilis* (13%), *Quadrula pustulosa pustulosa* (13%), *Simpsonaias ambigua* (13%), and *Elliptio crassidens crassidens* (7%). Calculation of faunal resemblance indices for Kinniconick Creek and other similar-sized streams in the Ohio River basin (Table 2) revealed a range of 46–76% with the strongest resemblance to direct Ohio River tributaries and the least resemblance to a Cumberland River tributary. Comparison of the fauna of Kinniconick Creek with seven other small to medium-sized Ohio River valley steams (Houp, 1980; Taylor, 1980a, b, 1981, 1982; Zeto, 1980; Starnes and Bogan, 1982) revealed that *Alasmidonta viridus*, *Obovaria subrotunda*, and *Lasmigona complanata* were present in 71%, 57%, and 57%, respectively, of the other streams but were not collected in Kinniconick Creek. Conversely, species present in Kinniconick Creek but not reported from a large percentage of other streams were: *E. c. crassidens* (86%), *Villosa lienosa* (86%), *S. ambigua* (71%), *E. triquetra* (71%), and *Q. p. pustulosa* (57%).

DISCUSSION

The occurrence of 20 species of bivalves in Kinniconick Creek (Table 1) compares favorably with other small to medium-sized streams previously surveyed in the Ohio River drainage (Table 2). The representation of all species in Kinniconick Creek by live specimens, most of which occurred at several stations, indicates a healthy, viable fauna and attests to the overall quality of the drainage.

Examination of the distribution pattern (Table 1) indicates longitudinal succession similar to that observed elsewhere for fish and invertebrate species (Kuehne, 1962; Harrell and Dorris, 1968; Starnes and Bogan, 1982). With few exceptions the distribution pattern consisted primarily of addition and/or replacement of species in a downstream direction. The most speciose and dense populations were observed in the generally moderate-gradient middle reaches of the stream (stations 5–10) (Fig. 2) with an increasingly depauperate fauna occupying the higher gradient upstream stations (11–15) and the region near the mouth (stations 1–4).

The diminution of diversity in the headwaters is consistent with observations of Starnes and Bogan (1982). Although there was no significant correlation between gradient and average numbers of species per segment, the data indicated a trend in the middle and upper segments toward decreased diversity at higher gradients as illustrated in Figure 2. A rapid decrease in number of species was particularly evident between stations 10 and 11. Other factors associated with gradient such as decrease in flow, stream size, and ultimately habitat heterogeneity are also probable factors in decreased diversity in upstream reaches.

The abrupt decline in number of species near the mouth of Kinniconick Creek (stations 1–4) was unexpected and represented an exception to the classical depiction of increased diversity along longitudinal gradients. Several plausible factors could be responsible for this observed distributional pattern. The influence of the impounded Ohio River on the lower reaches may at times of high water reduce flow, increase sedimentation, and inundate riffle-pool habitat. The lower gradient of Kinniconick Creek subsequent to its plunge onto the large Ohio River floodplain (Fig. 2) and the associated increase in alluvium may also have acted to reduce habitat heterogeneity and thus the number of species. Another possible factor is the increased anthropogenic influence on the floodplain. Although the collecting methods may have contributed to the lower number of species observed near the mouth, based on the preponderance of pool habitat and the factors previously discussed, it is believed that collecting methods alone could not account for the dramatic difference in diversity between the middle and lower reaches. In general, lowered diversity at any given station could be associated with a preponderance of pool habitat, unstable or shifting gravel substrates, extensive bedrock or large boulder substrate, and/or increased gradient.

Table 2. Total species and faunal resemblance indices for Kinniconick Creek and other small to medium-sized Ohio River basin streams.

Stream (Location)	No. Species	Faunal Resemblance (%)
Big Indian Creek (Ind.)[1]	17	76
Tygarts Creek (Ky.)[2,3]	22	76
Middle Island Creek (W. Va.)[4]	23	75
Floyds Fork Salt River (Ky.)[5]	20	70
Eagle Creek (Ky.)[6]	21	68
Red River (Ky.)[7]	15	58
Little South Fork Cumberland River (Ky.)[8]	24	46
Kinniconick Creek (Ky.)	20	—

[1]Taylor (1982); [2]Taylor (1980a); [3]Zeto (1980); [4]Taylor and Spurlock (1981); [5]Taylor (1980b); [6]Taylor (1981); [7]Houp (1980); [8]Starnes and Bogan (1982)

The fauna occupying Kinniconick Creek is, as expected, typically Ohioan. Faunal resemblance values (Table 2) indicate strong similarity among species assemblages in Kinniconick Creek and those occupying nearby direct Ohio River tributaries in Indiana, Kentucky, and West Virginia. Similarity of faunas decreases in those streams of the middle Ohio River valley which are not direct Ohio River tributaries. This suggests that the proximity of the Ohio River mainstem is an important factor in determining faunal make-up of small tributaries such as Kinniconick Creek. Of particular note is the low faunal resemblance between Kinniconick Creek and Little South Fork Cumberland River which illustrates that the disparity between the Ohioan and Cumberlandian pelecypod faunas (Ortmann, 1926) is apparent even in relatively small tributaries.

Habitat information provided in Ortmann (1919) and Parmalee (1967) for the bivalve species observed in Kinniconick Creek indicates that most are dependent on riffle habitat or current. Only a small number of the species present was associated with lentic environments. Two of the typically lentic forms, *Anodonta grandis grandis* and *Leptodea fragilis*, were restricted to the upstream and downstream reaches of the stream, respectively. The preponderance of riffle or rheophilic species with an admixture of lentic forms is to be expected in a stream like Kinniconick Creek which has good riffle-pool development and a variety of bottom types.

With the exception of *Corbicula fluminea* and *Lampsilis ventricosa*, all the other species denoted as common are typically associated with stream or small river habitats (Ortmann, 1919; Parmalee, 1967). *Lampsilis ventricosa* is also associated with big river habitats. *Corbicula fluminea* is a ubiquitous species which, since its introduction, is a common inhabitant of small streams to large rivers throughout

Kentucky (pers. obs.). The species was totally absent above station 6 in this study, although it was extremely abundant in the lower reaches of the stream. The factor(s) responsible for its inability to colonize the remainder of Kinniconick Creek are unknown; however, stream size and suitable substrate do not appear to be limiting. Of the species with limited distribution within the stream the presence of *Elliptio crassidens crassidens* is surprising because of its well-known preference for large rivers and strong currents (Ortmann, 1919; Parmalee, 1967). Its rarity in Kinniconick Creek and absence from most of the other streams previously cited (Table 2) further documents this preference. The presence of *E. c. crassidens* in Kinniconick Creek is most likely associated with the proximity of the Ohio River, and it probably has never been a prominent component of the Kinniconick Creek fauna.

Of particular interest was the occurrence of *Epioblasma triquetra, Villosa lienosa*, and *Simpsonaias ambigua* in Kinniconick Creek and their conspicuous absence from a majority of other previously cited streams of the Ohio River valley. In Kentucky, these species are recognized as of special concern, endangered, and of undetermined status, respectively, by the Kentucky Academy of Science (Branson et al., 1981). Their absence from other Ohio River valley streams could be attributable to an artifact of collecting. For example, Parmalee (1967) notes that *E. triquetra* is easily overlooked by collectors due to its habit of deeply burying itself. However, both *V. lienosa* and *S. ambigua* have been decimated in parts of their range (Parmalee, 1967) and populations in Kinniconick Creek offer continued hope for their persistence both in Kentucky and the middle Ohio River valley.

Kinniconick Creek represents a high-quality, relatively undisturbed middle Ohio River valley stream which to date has escaped all but low-impact watershed development. Aside from its diverse pelecypod fauna, the stream also supports a self-sustaining muskellunge (*Esox masquinongy*) population as well as a diverse ichthyofauna (Kornman, 1982, pers. comm.; Warren and Cicerello, 1983). Based on its biological merits, the stream was recently recommended for inclusion as an Outstanding Resource Water in Kentucky (Hannan et al., 1982). Unfortunately, the future maintenance of these qualities is uncertain due to recent investigations into the feasibility of extracting oil shale deposits located in the watershed. The resultant surface mines, inevitable increase in siltation, and potential for acid run-off threaten not only the indigenous unionid fauna, but also the integrity of the entire watershed. Continuing efforts by state agencies, interested academicians, and researchers will hopefully help to preserve Kinniconick Creek and its fauna.

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S. STILLMAN BERRY (1887–1984): A TRIBUTE THROUGH GLIMPSES AND REFLECTIONS[1]

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ABSTRACT

Dr. S. Stillman Berry (1887–1984), Honorary Life President of the American Malacological Union, is honored through a brief biographical summary. The tribute is based primarily on stories told by Berry and on the author's experiences with Berry. The multifaceted nature of Berry is addressed: the scholar/malacologist, the horticulturist, the rancher/businessman, the genealogist, the bibliophile, the mentor.

With the death of Dr. S. Stillman Berry on April 9, 1984 at age 97, the American Malacological Union lost its Honorary Life President, malacology lost a dedicated scholar, and many of us lost a dear friend. The purpose of this paper is to honor and remember Stillman Berry by presenting some glimpses and reflections as a tribute to him and his long, productive life.[1] The primary sources of information presented here are two: (1) Stillman Berry himself, through my recollections of the many stories he told over the years we were friends; any deviations in facts are my memory failings, not his—I never knew him to change any facts in his stories; (2) my personal experiences enriched by nearly twenty years of knowing him and visiting him in Redlands, California and in Montana; other sources are listed under References. Many friends could present such a paper, but all presentations would be different because of personal experiences with Stillman. All would be bound by a common thread, however; none of us affected his life to any signficant degree, but he certainly affected each of our lives in various, often very significant ways. A major reason for this is that Stillman Berry was a consummate and dedicated teacher.

Among my reasons for giving this tribute are that Stillman Berry was an extraordinary malacologist, a scholar nearly unique in the 20th century; he was the only Honorary Life President of the American Malacological Union, having been elected in 1960; he was a Research Associate of the Smithsonian Institution, a relationship of which both he and we were proud; he was the only Honorary Member of the recently chartered Cephalopod International Advisory Council (CIAC) in honor of his monumental contributions to the knowledge of the cephalopods of the world.

I first met Dr. Berry during a visit to the Smithsonian's National Museum of Natural History in December 1965. I had gone there to work out some sticky problems associated with my dissertation on *Bathyteuthis*, a deep-sea cephalopod, and he was there checking up on his old cephalopod types and examining recent cephalopod collections. I was already at work and had been aware that someone had entered the room and begun puttering in the cubicle across the table. Joe Rosewater came in to see if I had everything I needed and chatted for a couple of minutes. No sooner had Joe left when a head and torso bobbed abruptly around the separating bookcase and a thin, bespectacled old man demanded, "Who are *you*, young man, and where in New Hampshire do you come from?" I told him. "I thought so; I'm Stillman Berry and one of my ancestors settled Rye." He had seen that I was working on squid, had heard my accent, and couldn't wait to find out the story. Of course, as a graduate student who had used so many of his cephalopod works and had heard so much about him, I was delighted. That began a marvelous week or so during which we became well acquainted, had lengthy discussions about cephalopods, New England genealogy, American malacologists, and cephalopod workers from around the world who he knew or with whom he corresponded. He was staying at an old hotel up near Union Station, quite some distance from the museum. I tried to persuade him to move down to the Harrington where I stayed, as it was only a couple of blocks from the museum and also quite inexpensive. Washington in the mid-60's wasn't the safest place to walk around in late in the evening. He brushed away my concerns, refused to take a bus or taxi, and insisted on staying where he'd always stayed starting decades ago! I walked home with him each evening and met

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[1] This paper was presented at the Annual Meeting of the American Malacological Union in Norfolk, Virginia in July 1984. Obituary notices have been published by Brookshire (1984) and Coan (1984).

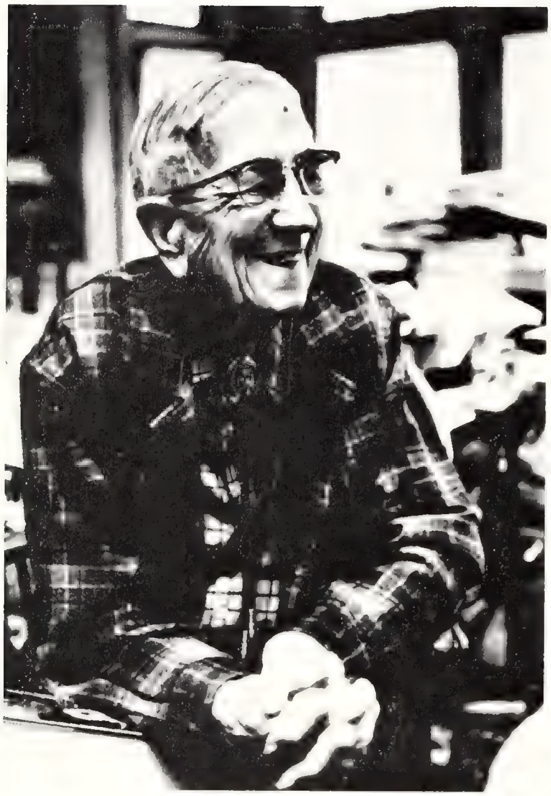

Figure 1. S. Stillman Berry on his 95th birthday, 16 March 1982. (Photo, Chuck Painter)

him each morning. Wonderful conversational walks they were, punctuated with historical facts about old buildings we passed or comments about when Hoover was president or "that horrid FDR." I began to learn he had strong likes and dislikes!

One of my objectives while visiting the museum was to try to establish which generic name had priority: *Benthoteuthis* Verrill, 1885, or *Bathyteuthis* Hoyle, 1885. I was delighted to be with such a helpful nomenclatural expert as Dr. Berry. Later, after I had worked everything out, I wrote to him with the details and the decision—*Bathyteuthis* Hoyle by a couple of months. He replied that he could accept my findings based on facts, but he would have "much preferred" it be Verrill's name for patriotic and linguistic reasons. During our discussions of *Bathyteuthis* I was alarmed to learn about "my [Stillman's] species from California waters," which was all described, illustrated and ready to be published. I was very interested to know the publishing details, of course, because I had a large series of the same species and wanted to refer to Berry's name and the correct citation without pre-publishing on him. As it turned out, he needed males, more illustrations, and typing. It became clear after later correspondence that Berry would not be able to publish within a reasonable time and that I would have to publish "his" species along with the rest of my *Bathyteuthis* work. My guilt was partially assuaged by naming the species *Bathyteuthis berryi.* I think this rather pleased Stillman Berry because it both honored him and relieved him of the responsibility of having to get that description out (he was, after all, nearly 79 years old at this point). I understand from some malacologists older than I that in former times such a "threat" to a prospective Berry species would be met with instant publication in the *Nautilus* or *Leaflets in Malacology*.

Samuel Stillman Berry was born in Unity, Maine, on March 16, 1887, his mother having returned from the family ranch in Montana for the delivery. Stillman was the second-born of twins, a surprise arrival who was so scrawny and weak-looking that he was placed on the windowsill so full attention could be paid to the robust, healthy-looking first-born twin brother. That icy March Maine windowsill probably did more for stimulating those first deep breaths than any midwife's slaps on the bottom ever could! At any rate, a doting aunt finally took notice of the waif, wrapped him up and did whatever they did to babies in 1887. Ironically, the robust baby died shortly after birth and Stillman, with the aid of a homemade incubator, survived. Stillman's early childhood was a search for health during which time the very sickly child was moved from Maine to Montana, New York, Minneapolis, Phoenix, Santa Barbara, Pasadena, and finally, in 1897 when Stillman was 10 years old, to Redlands, a climate the doctor had insisted was the best in the country for the child. Something must have been right, as Stillman Berry remained in Redlands for the ensuing 87 years of his life.

An incident when Stillman was three years old is worth retelling. The Berrys had learned about a famous physician in Minneapolis who was an expert at performing modern medical procedures. Very anxious about their young son's health, the Berrys decided to engage the learned doctor. The doctor determined on the first visit that the little boy's adenoids had to come out, and no time like the present to perform this simple modern procedure. Without administering anesthesia, the doctor inserted a looped wire around the swollen adenoids and yanked them out. We can understand why the tears welled in Stillman's eyes decades later in recalling one of his earliest childhood memories as he still felt the pain and saw the large, white porcelain bowl filling with his own blood. Stillman survived in spite of the operation and the massive loss of blood, but he had a hard time liking doctors for many years afterwards!

Stillman Berry's early education was sporadic at best. Because of his poor health he was forced to miss much of his classroom schooling. In fact, he completed only three full years of elementary school. He kept up his lessons, with guidance and tutoring from his mother and aunt, to the extent that he was allowed to skip two grades. In Redlands High School, Stillman founded the Year Book and, not being able to participate himself, became an avid sports fan, an interest he carried throughout life. Immediately after graduating from high school in 1904, Stillman, his mother, and his favorite teacher sailed for Europe where they spent the next full year traveling from Scandinavia to Greece. This experience had a great influence, as he was exposed to a broad cultural education that can be gained no other way—history, art and architecture, music, theater. All experiences are vividly recorded in neat daily diaries and with many albums of photographs. It turned out to be Stillman's only trip to Europe, but he certainly made the most of it and remembered every detail of his tour.

Stillman Berry's undergraduate work was taken at Stanford University, where he majored in biology but took and enjoyed many other courses, including several in law. Stillman very much enjoyed campus life and extracurricular activities including hiking, camping, and dancing, the latter attested to by his having saved all the colorful dance cards, slender little pencils still attached, every numbered dance filled in with the name of a dancing partner. Among the dance cards is a note from his cousin acknowledging Stillman's expressed excitement about an upcoming dance and the possibility of dancing several times with a particular young lady.

Stillman was a freshman in the spring of 1906 when the great San Francisco earthquake struck at 5:13 a.m., April 13th. Shaken from sleep, Stillman grabbed a few things and amidst the roar, fled the building, narrowly missing the falling debris as he ran out the back door of Encina dormitory. Although still in nightshirt and slippers, he carried his clothes, shoes, books for his early morning German class, and camera without film. Later on, with his best friend Stanford B. Dole, II, he roamed the campus, photographing the devastation; the extensive album is still intact, a vivid reminder of that traumatic experience. A story Stillman delighted in retelling, as a demonstration that out of chaos can come humor, concerned the large statue of the early American oceanographer and marine biologist, Louis Agassiz. The quake dislodged the statue and it dove head-first into the concrete sidewalk where it rested unbroken and upright on the shoulders, feet to the sky, a comical sight that prompted comments about Agassiz's hardheadedness and penetration. The capper came when the visibly shaken University President, David Starr Jordan, happened by, saw the inverted statue and observed that he always knew that Agassiz "was very fine in the abstract, but he's no good in the concrete." Berry's several-day trek home by train and on foot was an adventure in itself, told along with other details in an article that appeared in the *Stanford Campus Report* (Stokes, 1982).

Following graduation in 1909, Stillman Berry went to Harvard for a Master's degree. There he began his work on cephalopods in earnest and had the joy of meeting at Yale, A. E. Verrill, the grandfather of American cephalopod research. Already a burgeoning bibliophile, Stillman haunted the old book stores of Cambridge and Boston, picking up some "nice things for only pennies." On one such excursion in Boston he passed by the exclusive grocery store of S. S. Pierce, where a man was setting up a display of magnificient oranges in the window. Stillman marched in and asked, "Which grove in Redlands do those oranges come from?" The man confirmed what Stillman already believed: they were from Redlands and S. S. Pierce used them because they were the "best navel oranges in the world." What a wonderful touch of home that must have been for someone so far removed from home and family. At Harvard commencement exercises of 1910, Stillman was selected to represent all the students earning Master's degrees. He never forgot the honor of sitting on stage between President Teddy Roosevelt and later to be Chief Justice Charles Evans Hughes, then Governor of New York, and, of course, he remembered every detail of their conversations.

Stillman Berry returned to Stanford for his Ph.D. studies, where he worked under Professor Harold Heath. His dissertation on the cephalopods of western North America was a masterful work that remains a classic in cephalopod literature to this day. The Ph.D. was conferred in 1913.

During Berry's eight years of education away from home, he maintained virtually a daily exchange of correspondence with his mother and aunt. All these letters are still extant in a large trunk along with hundreds of others; together they constitute a rich resource of information about the man and his family going back to the 1850s in Maine.

One of the many stories I never tired hearing concerned Berry's employment at Scripps Institution of Oceanography, then called the Scripps Institution of Biological Research. Professor Heath was approached in 1913 by Ellen Browning Scripps who was seeking recommendations for someone to set up the library at Scripps. Without hesitation Heath "allowed as how" there was only one person in the country whom he could recommend with the biological training and the great breadth of knowledge of the scientific literature. That was S. Stillman Berry. So Stillman Berry was hired as librarian to build the library at Scripps at a salary of $300 per year. He was allowed to work overtime for extra pay of 35 cents per hour, limited to three hours a week. E. W. Scripps provided $10,000 to purchase books and Berry, being a good New Englander, determined to make that go as far as possible. Europe was in the middle of World War I and a severe economic depression during this time. Many of the wonderful old libraries were being broken up and sold through antiquarian dealers at bargain prices. Berry conducted business with virtually every book dealer of note in Europe, especially in England and Germany. He had placed a huge order with a Berlin antiquarian dealer when the British imposed on Germany a complete blockade to shipping. There sat the books that were to form a major portion of the Scripps library, with no indication when the blockade would be lifted and even then, if the books would be shipped. Stillman reared up his scholarly indignity and approached the appropriate officials in the United States and British governments, who in turn conducted delicate negotiations with the German government. Finally, the British Admiralty agreed to lift the blockade for a very specific time period and to allow a single, designated ship to pass. That ship carried crates and crates of books around Cape Horn and into San Diego. The books arrived at Scripps without so much as a water spot and they form the basis of one of the most extensive and complete oceanographic libraries in the world. Thanks to Berry the Blockade Buster!

Interestingly, that job at Scripps was the only professional position Berry ever held.

During the five years (1913–1918) Berry was librarian at Scripps he had the opportunity to purchase books for his personal library that were duplicates of Scripps holdings or otherwise not needed. As his primary research interest was and always remained the cephalopods, works related to this group were his top priority, followed by chitons, land snails, and finally, general malacology and general natural science. Even with his overtime income, Berry's penchant for buying books placed a severe strain on his budget to the extent that he frequently went without lunch in order to pay for his books. Over the decades and into 1983 Berry continued to purchase books and ultimately amassed one of the best private libraries of its kind in the country.

A career quite aside from teuthology (the study of cephalopods: squids, octopuses, cuttlefishes) and malacology occupied a significant portion of Stillman Berry's attention—the running of Winnecook Ranch near Harlowton, Wheatland County, Montana. Stillman's father, Ralph, and an uncle, Ralph's brother, left Unity, Maine, for "better pickin's" in the west; they eventually settled in Montana Territory where they founded the 65,000-acre Winnecook Ranch in 1880, named after their favorite lake, Winnecook Pond, near Unity. Stillman's father went to the west coast to pick up the shipment of several thousand Merino sheep. With the assistance of a single Basque sheepherder, Ralph Berry drove one of the first herds from Nevada across the mountains and into Montana, an impressive feat of endurance and skill. At one point Berry was surrounded by hostile Indians who threatened to steal his sheep; he quickly slaughtered a fat ewe and gave it to the Indians, who then departed, satisfied with their next meal. During those first years, that part of Montana was still Indian Treaty lands where several tribes had hunting rights. I was fortunate to be able to visit Winnecook with Stillman in 1973. He was in peak pedagogical form as he recounted the history of the ranch. His parents witnessed the final Indian buffalo hunts at the buffalo falls, a cliff over which the beasts were driven and slaughtered. We looked down on the little valley from atop the falls and saw numerous rings of large stones laid out by the squaws to hold down the hides for scraping and tanning. Bleached bison bones still lay all about and stone scrapers were common. Several Indian skirmishes took place on the ranch, one just outside the log cabin where Stillman's mother, Evelyn, and a young girl helper were alone. They blockaded the door and poked rifles out every window, then made the rounds frequently, moving the rifles so the Indians would think the cabin was filled with marksmen. The great Chief Joseph made his escape into Canada across Winnecook lands. Winnecook Ranch is bisected by the Musselshell River, a tributary of which provided Stillman with a study site for long-term observations of colonies of beavers, their canal building and maintenance, the first such ever published (Berry, 1923). Winnecook also is the type locality for a number of fossils. We visited many fossil sites and collected fossils, including cephalopods—nautiloids, ammonites, belemnites—dinosaur gizzard stones, and Indian stone artifacts. All this activity was accompanied by a constant litany of historical facts, geological and paleontological lessons, Indian lore, and sheep and cattle ranching theory and practice.

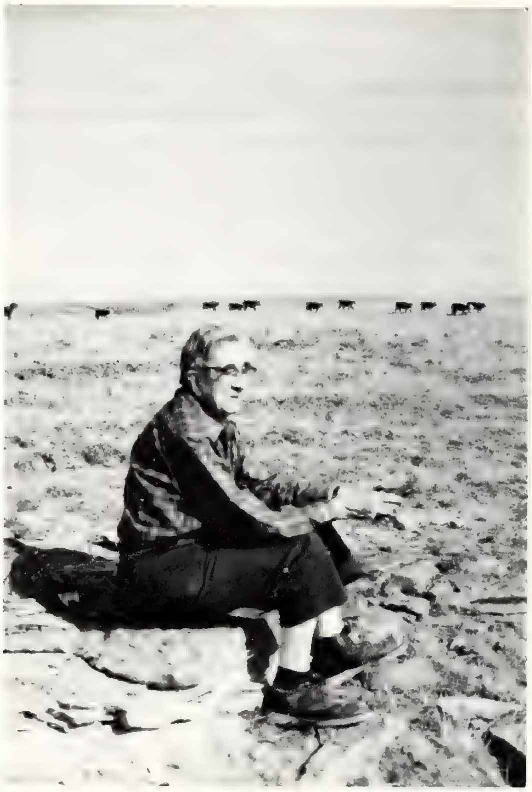

Figure 2. S. Stillman Berry at Winnecook Ranch, Montana, in August 1973. (Photo, Clyde F. E. Roper)

At one point, up in the northern section of the ranch, Stillman had tired and sat down on a comfortable rock to rest and watch the cattle and distant antelope, letting my son, Erik, then eight years old, Ingrid and me wander off in search of treasures. Ingrid eventually tired as well and said she was going back to talk with Stillman. We had circled around in a broad arc, so her approach was from behind Stillman and up over a steep slope. Before spotting him she heard what at first sounded like rhythmic moaning sounds, but as she drew near she recognized the strains of an old German folk song being sung at full volume. When Erik and I returned an hour or so later, Stillman was still holding forth, entertaining Ingrid with all the old songs he had learned in Europe, in near-perfect tune and perfect pronunciation, regardless of language! Not bad for an eighty-six-year old!

Stillman Berry was a member of the Winnecook Ranch Board of Directors for 73 years since his father's death in 1911, and also was President of the corporation for 67 years from 1917, positions he held until his death. Surely these are records in American corporate history.

The Berrys lived on Cajon Street in Redlands from 1897 until they moved up to West Highland Avenue in 1913. On this very productive small acreage Stillman Berry maintained an orange grove and raised 97 varieties of fruits and nuts, some of them quite exotic. Here, too, a second career blossomed—that of Stillman Berry, the horticulturist. He was a recognized world authority on daffodils and irises and is credited (Brookshire, 1984) with developing 2,700 varieties of these two groups of flowering plants (I have been unable to verify this figure, and I don't recall Stillman ever telling me). Stillman was justifiably proud of his horticultural and gardening skills and he told me that for many years his small property reported the highest per acre yield in California. State agricultural agents visited frequently and verified Stillman's figures. In this activity, as in his malacology, his ranching business, his genealogical studies, he kept meticulous notes and records. The production from these 2 acres provided the income that sustained the Berrys for many years while the ranch was barely keeping apace.

In 1914 Stillman Berry was elected to the Fortnightly Club of Redlands, an old, honored literary society. Stillman presented numerous papers during his lifelong tenure with the society, of which he was, since 1955, the Honorary Life President.

The Berry home in Redlands very early became the center of attraction for young people interested in natural history. Stillman was a teacher of the highest order, *outside* the classroom where lessons of life were interwoven with the zoological and botanical topics. From his own youth onward Stillman took a keen interest in helping students; the first was Allyn Smith, later an associate of the California Academy, followed through the years by over a hundred who proudly called themselves one of "Stillman's Boys." Many have gone into various fields of biological science, but many fields, other sciences, the professions, and business are represented by Stillman's Boys. I venture to say that every one of them, regardless of his chosen field, will readily credit Stillman Berry with playing a significant role in his development as a young man. His interest in them certainly was keen, sincere, and everlasting, and he followed their lives and careers with warm enthusiasm. Little wonder that the Berry homestead was called the "B-Hive" and "Berry U."!

Anyone who ever visited Dr. Berry's home will never forget it, inside or outside. The front yard is graced by a single magnificent redwood tree, now huge, but planted from a coffee can by Stillman on Armistice Day, 1918, in memory of a cousin killed in the World War. California state foresters claim that that tree is the largest known for its age on record; they visited annually to measure its growth. Stillman was so proud of Redlands; in fact, his unswerving loyalty had a comical bent. I recall one visit in the summertime when I took him for a ride in the mountains outside of Redlands. On the way home we stopped at an overlook to admire the San Bernardino Mountains, Mt. San Gorgonio, and Cajon Pass. He was thrilled at the scene and the air. "You know," he told me, "Redlands doesn't have any smog. It comes out the valley and *stops* at San Bernardino." As though smog wouldn't *dare* penetrate Redlands. This was followed by a little dissertation on why this was so. I didn't have the heart to ask him why my eyes were burning so. I took a photo of proud Stillman with the mountains and the valley in the background; I *knew* the valley had to be there somewhere!

The longer I knew Stillman Berry, and with each recurring visit, I learned what a truly remarkable man he was. First off, he was a true scholar, almost in the Renaissance sense. He knew ten languages, including Greek and Latin. He was an avid student of history, art, music and literature. We, from the perspective of AMU, think of Stillman Berry as a malacologist; many see him as a teuthologist, some as a chiton specialist, someone else as a West American land snail expert, others as an eastern Pacific marine malacologist, etc. He was *all* of these as a malacologist. Berry's first mollusk paper was published in 1906 on the genus *Cerithidea*, and he continued publishing for seventy years, with his last paper appearing in 1975 on the pelagic octopod *Ocythoe*. During his career as a malacologist Stillman Berry published 207 titles and described 401 new taxa (Sweeney and Roper, 1985). This is a truly incredible achievement for someone who never held a professional position in his field.

Stillman attended his last AMU meeting in San Diego in 1975. Ingrid and I had visited with him for a few days in Redlands; much of the time was spent in hunting down material for the paper he was scheduled to present. He had slowed down by then and it was easier for me under his direction to dig out specimens from the dining room closet and the basement, books from the corner room, reprints from the back room, notes from the landing, and illustrations from the land snail cabinets. Only those who have seen Berry's 17 room house in the past 2–3 decades can appreciate the challenge this presented. The drive down to San Diego was an experience in itself. We avoided all freeways and stuck to the back roads as much as possible. The entire journey was a naturalist's travelogue during which Stillman pointed out type localities for myriads of plants and animals, early collectors and their important collecting sites, geological history, paleontology, his own adventures here and there, Indian and Spanish history. At one point we passed a huge flower plantation and Ingrid exclaimed, "Look at all the gladiolus" (long o), whereupon Stillman swung around in his seat and said, "My dear, those are gladiolus" (long i). Then he commenced a lecture on the rules of Latin governing the correct pronunciation of that flower, *Loligo, Octopus*, and margarine (hard g) of all things. He didn't see the humor when I asked him if "garage (hard g) was correct; in fact, he quite properly ignored that comment and went right on with the lesson!

That '75 AMU meeting was memorable on several counts. It was the last time three west coast malacologists were together: Stillman Berry, Joshua Baily and E. P. Chace. I figured their aggregate ages totalled around 270 years. What a sight it was to see them all together! Stillman presented his last paper at those meetings, and quite appropriately it was on a cephalopod, the pelagic octopod *Ocythoe*. He had told me that he felt this would be his last paper and he very much wanted it to be on cephalopods. He mentioned

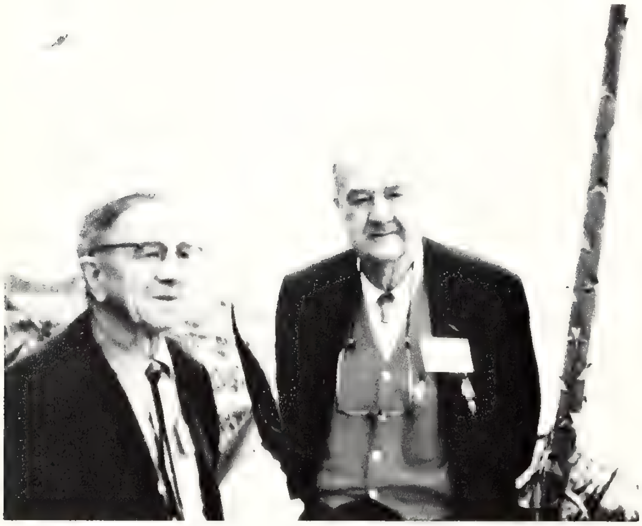

Figure 3. S. Stillman Berry and Joshua Baily in San Diego in 1965. (Photo, Eugene Coan)

then, as he did on several occasions over the years, that the cephalopods were his favorite group of mollusks and that had he worked at an institute or museum they would have been his exclusive research group. However, working independently as he did, and living in an area where the molluscan fauna still required much delineation, he felt compelled to do what he could to improve the knowledge of other molluscan groups in addition to cephalopods, especially his "second favorites" the chitons and then the land snails.

We have mentioned Berry's prowess as a horticulturist; tied to this were interests in botany, gardening, and English gardens, all subjects in which he also published numerous papers, including some on desert flora with Edwin Jaeger, the famous desert botanist. Another interest of Berry's was genealogy, "that's pronounced gĕnealogy (short e, not long e); it's the study of your generations, not your genes!" He was considered a national expert on New England genealogy. Whenever he met someone for the first time he would immediately determine where they were from and what was known of their ancestry.He was fond of trying to find connections between his ancestry and that of someone he liked, including teuthologists. For example, he was fairly certain there was a distant connection with Gil Voss, whose ancestors had been Mainers since they came to this country. He told me he tried hard to find a Berry relationship with Roper, as Ropers and Norcrosses (my maternal lineage) go way back in Massachusetts and Maine history (it was all Massachusetts back then), but he never did, at least not that he would admit to!

Through genealogy he also was a historian, especially of New England and western America, because of its settlement by New Englanders.

Finally, Stillman Berry was a bibliophile supreme. His magnificent library reflects the very broad range of fields mentioned above. His extensive library ultimately became stored throughout the entire house, including hallways, stairs, floors, closets—everything with a horizontal surface became a fair resting place for books and reprints. What once must have been good order eventually became total disarray. In recent years Stillman had many interests and projects going on simultaneously, or someone would stop by for a visit with a special specimen and he would pull books and papers appropriate for the moment. Then, before he had a chance to put them away, something else came up, until eventually it became an impossible task to keep order. Stillman maintained a strong interest in literature throughout his life and still received all the antiquarian catalogues which he would scrutinize to see if there were anything he needed to fill in gaps or shake his head aghast at the prices they were asking for items that he picked up for only a few dollars years before, or laugh in dismay at what they were charging for *his* papers!

A few years ago we were having a conversation when he said, suddenly, "You know, Clyde, I don't have any sins!" I wasn't going to get into that one so nodded for him to continue. "I don't drink, never have. I don't smoke. (Woe be to anyone who ever did in his presence or in his home!) I've never been married." (*That's* a sin?) He paused pensively, then with that special little twist of the head that was uniquely Stillman, he confessed, "Well, I do have *one* sin. My *only* sin is buying books!" That being the case, Stillman Berry was a sinner of the highest order!

Berry was a man of strong likes and dislikes. While we won't go into them all here, he intensely disliked government and the Democratic Party, and if you had an extra hour or two, just mention FDR! These dislikes developed naturally enough through what he viewed as the interference and over-regulation of government, and especially the Roosevelt administration, concerning the ranching business. Berry fought most of his life to maintain Winnecook Ranch as a free enterprise, free from government loans, subsidies, takeover. His likes were many. He loved animals and wouldn't tolerate harm to any; he allowed no hunting or trapping on Winnecook and had a difficult time accepting the predator control program on coyotes. If they *had* to control coyotes, he didn't want to hear about it. He loved cats and always had one or more around, completely tolerant of their misdeeds. He was especially attached to his last two in succession, Purry Boy and Fluffy. Food: Stillman loved certain foods, but, living alone for so many years he had developed some peculiar eating habits. Crackers were his staple; only two kinds were worth eating—Pilots and saltines. Crackers and milk could be any meal of the day or every meal, if necessary. He saved every cracker box he ever had, too (along with every letter, card, rubber band, piece of string, "tin" foil and "butter" tub!). He used them for specimen boxes. For years they were stored in the north end of his kitchen, floor to ceiling, 3–4 layers deep.

One year I visited him in June and out behind the old cook house I discovered his raspberries in full production. I picked several quarts, then asked Stillman what his favorite raspberry dish was. "Pie," he replied, "although gooseberry is my favorite pie." So I made three huge raspberry pies and that's all we ate for the next two days, the only variable being coffee for breakfast, milk for lunch, and tea for supper—Earl Grey or Darjeeling.

Stories about Stillman's house could go on forever, but there is one thing worthy of note—in spite of the incredible amounts of papers, newspaper clippings, correspondence, envelopes, etc., piled and heaped everywhere in the house (the 1938 material was on a table in the dining room, the pile of '62 papers in the back corner of the living room, etc.). I never saw evidence of insects, except in the kitchen, of course, where generations of ants subsisted on the kitchen table and counter top. The reason: Stillman kept his own living pest control system—spiders. He wouldn't kill a spider and wouldn't allow anyone else to, either. They kept the undesirable insects under control. This empathy for spiders goes far beyond the pragmatic aspects of "natural hygiene." It goes back to the French and Indian War when two soldiers from the Maine regiment were the only ones to escape the Indian massacre on a fort of solidiers and civilians in western New York State. Some Indians noticed the two disappearing into the forest and took off in hot pursuit. One soldier eventually tired, fell back and was captured and killed. That gave the survivor time to press on 'til the point of collapse. With the Indians again in pursuit, he was about to give up when he sighted a large hollow log. He carefully covered his trail and wiggled as deep into the log as he could. The Indians soon came upon the scene; some were tired and sat on the log, while the trackers tried to work out the trail. One insisted that the quarry was in the hollow log, peered in, then suggested they light a fire to smoke him out. Another pointed out that that was impossible because a spider web was stretched across the opening; anyone entering would have broken it. "And the longer we wait, the farther he runs." His argument prevailed and the war party went off. The survivor remained in the log for nearly two days, then with great travail eventually made his way back to Maine. That soldier was a direct-line ancester to Stillman Berry, and Stillman figured if it hadn't been for that quick spider 250 years ago, he wouldn't be around to tell the story or to protect spiders. What a twinkle in his eyes whenever he told that story!

The last few days of Stillman's life serve to demonstrate the kind of person he was. From Christmastime 1983 into early January 1984 Stillman had a series of small strokes that left him weak but which primarily affected his speech. He had some difficulty finding the right words and in pronouncing some words. Confined to bed, he instructed his housekeeper/nurse of three years, Alexandria Luzell, to fetch his old Greek grammar text. He spent hours restudying his Greek in order to improve his speech and vocabulary!

Then, in late March, Alexandria drove Stillman out to the desert beyond Redlands so that he could see the spring flowers in full bloom. He sat among them, reciting their scientific names, authors, notes about their biology, and recounted anecdotes and reminiscences of his many trips to the desert, mountains, and sea. His joy was intense. Some time after returning home he told his long-time, dear friend and neighbor, Paul Allen, "Now it's time to move on and make room for someone else." His way. His time.

Who could ask for more than that?

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Coan, E. 1984. S. Stillman Berry, 1887–1984. *The Veliger*, 27(1):99.

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Stokes, D. 1982. Freshman who lived through '06 quake tells his adventure. *Campus Report*, Stanford University; April 14, 1982.

Stuck, N. 1984. Stillman Berry dies at 97. Redland's Daily Facts, 9 April 1984.

Sweeney, M. J. and C. F. E. Roper 1984. The Zoological Taxa and Bibliography of S. Stillman Berry. *American Malacological Union Bulletin* [this volume].

Times Clarion, Harlowton, Wheatland County, Montana. Dr. Berry dies in Redlands, California, 19 April 1984.

THE ZOOLOGICAL TAXA AND BIBLIOGRAPHY OF S. STILLMAN BERRY

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With the recent death of Samuel Stillman Berry (16 March 1887–9 April 1984), the field of malacology lost one of the last independent, multi-disciplinary scholars of the twentieth century. His interests, however, were much broader than just malacology and included such diverse subjects as marine and terrestrial natural history, genealogy, horticulture, philately, classical languages, bibliophily, paleontology, petroleum geology and 19th century naturalists. Short biographies and anecdotes of Berry can be found in Howard and French (1973), Brookshire (1984), Coan (1984), and Roper (this volume).

Stillman Berry's zoological publications were concentrated in three groups of mollusks: chitons, cephalopods, and land snails. He had no remunerative affiliation with any museum or university and worked from his home in Redlands, California. He relied on his own boundless enthusiasm, his meticulously curated collection, and his magnificant library to provide the stimulus and resources for his research. During his 70 years of publishing, Stillman Berry erected 401 names for mollusk taxa, a truly impressive record for someone relying mostly on his own resources. Many of these taxa were described in his privately published journal, *Leaflets in Malacology*. Most taxa described in *Leaflets* were not illustrated by Berry, but photographs of all have been published by Hertz (1984). Berry published a total of 209 zoological titles, the great majority on mollusks, but also on sparrows, magpies and beavers as well. Only three papers were jointly authored.

This paper presents a list of the zoological publications of S. S. Berry and includes the new taxa he introduced, as well. A number of sources were searched in order to make this as complete a bibliography as possible. Berry's own file card system of his publications formed the starting point, but it was found to be only about 75% complete, and, quite to our surprise contained errors and omissions in citations. The bibliography presented in the Howard and French (1973) paper appears to have been prepared from Berry's card file. The *Zoological Record* for the years 1905 to 1980 was searched, as were bibliographies in Berry's major papers, the card files of the Division of Mollusks Library, and the tables of contents of the American Malacological Union and Western Society of Malacologists publications. The summary of publication dates and volume numbers for the *Bulletin of the American Malacological Union* published in *Malacological Review* (1981, 14:67–70) by J. B. Burch was very helpful.

The bibliographic section lists the publications in a standard format, and, as an additional aid to nomenclatural studies, includes the day and month of publication, whenever they could be established. Researchers interested in determining dates or priority should verify these dates. Some journals such as the *Annals and Magazine of Natural History* (now *Journal of Natural History*) do not give day of publication and are listed with month only. Material enclosed in brackets [ ] is supplementary information added by us to clarify citations. The citation is followed by a list of the new names introduced by Berry as they originally appeared (e.g., hyphenated names). Papers presented by Berry at malacological meetings but not published other than by title are listed with the notation "[Title only of presented paper]".

Berry's taxa are presented in two indices. The first is an alphabetical listing of all proposed names; specific or subspecific names are followed by the associated generic and subgeneric or specific names. The second index lists supraspecific taxa alphabetically, and includes all taxa described by Berry and the year of publication; subgenera are enclosed in parentheses; species and subspecies are retained in the genus in which Berry originally placed them regardless of subsequent nomenclatural changes.

We would very much appreciate learning about any omissions or errors in the bibliography and the lists of Berry taxa so they can be included in a subsequent publication.

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Hertz, C. 1984. Illustration of the types named by S. Stillman Berry in his "Leaflets in Malacology." *Festivius* 15(Supp.): 1–42.

Howard, R. B. and R. C. French 1973. S. Stillman Berry—compleat amateur. *The Tabulata*, 6(2): 3–6, 18–22.

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ZOOLOGICAL PUBLICATIONS OF S. STILLMAN BERRY

1906, Apr. 5

Berry S. S. Note on a new variety of *Cerithidea sacrata* Gld., from San Diego, Cal. *Nautilus* 19(12): 133, 1 text fig.

Cerithidea sacrata hyporhyssa n. var.

1907a, Jun. 12

Berry, S. S. Molluscan fauna of Monterey Bay, California. *Nautilus* 21(2): 17–22.

1907b, Jul. 6

Berry, S. S. Molluscan fauna of Monterey Bay, California. [cont.] *Nautilus* 21(3): 34–35.

1907c, Aug. 16

Berry, S. S. Molluscan fauna of Monterey Bay, California. [cont.] *Nautilus* 21(4): 39–47.

1907d, Sep. 18

Berry S. S. Molluscan fauna of Monterey Bay, California. [cont.] *Nautilus* 21(5): 51–52.

1908a, Jan. 3

Berry, S. S. *Murex carpenteri*, form *alba*. *Nautilus* 21(9): 105–106.

Murex carpenteri form *alba* n. var.

1908b, Mar. 7

Berry, S. S. Molluscan fauna of the San Bernardino Mountains, California. *Nautilus* 21(11): 121–123.

1908c, Sep. 5

Berry S. S. Miscellaneous notes on Californian mollusks. *Nautilus* 22(4–5): 37–41.

Nassa perpinquis, var. *bifasciata*, nov.

1908d, Nov. 14

Berry S. S. Martyn's Universal Conchology. *Nautilus* 22(7): 72.

1909a, Nov. 13

Berry, S. S. The known Mollusca of San Bernardino County, California. *Nautilus* 23(6): 73–79, pl. 6.

1909b, Dec. 30

Berry, S. S. Diagnoses of new cephalopods from the Hawaiian Islands. *Proceedings of the United States National Museum* 37(1713): 407–419, 9 text figs.

Polypus hoylei n. sp.
Stephanoteuthis n. gen.
Stephanoteuthis hawaiiensis n. sp.
Stoloteuthis iris n. sp.
Abralia astrosticta n. sp.
Chiroteuthis famelica n. sp.
Cranchia (*Liocranchia*) *globula* n. sp.
Helicocranchia fisheri n. sp.

1910a, Mar. 8

Berry, S. S. [Review of] Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian Zoological Province. By W. H. Dall; *Proceedings of the United States National Museum* 37: 147–294, 1909. *Nautilus* 23(10): 130–132.

1910b, Oct. 1

Berry S. S. Mollusks of Unity, Maine. *Nautilus* 24(6): 61–63.

1910c, Oct. –

Berry, S. S. and E. L. Mark. Luminous organs in a cephalopod. [Title only; Eighth International Congress Graz, Austria] *Science* (N.S.) 32(824): 503.

1911a, Jan. 17

Berry S. S. A new sepiolid from Japan. *Zoologischer Anzeiger* 37(2): 39–41, 1 text fig.

Stoloteuthis nipponensis n. sp.

1911b, Apr. 6

Berry S. S. A note on the genus *Lolliguncula*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 63 [Feb.]: 100–105, 7 text figs., pl. 6.

1911c, May 31

Berry S. S. Preliminary notices of some new Pacific cephalopods. *Proceedings of the United States National Museum* 40(1838): 589–592.

Cirroteuthis macrope n. sp.
Eledonella heathi n. sp.
Polypus californicus n. sp.
Polypus leioderma n. sp.
Rossia pacifica n. sp.
Loligo opalescens n. sp.
Galiteuthis phyllura n. sp.

1911d, Sep. 20

Berry, S. S. Notes on some cephalopods in the collection of the University of California. *University of California Publications in Zoology* 8(7): 301–310, 4 text figs., pls. 20–21.

1911e, Oct. 3

Berry, S. S. A new Californian chiton. *Proceedings of the Academy of Natural Sciences of Philadelphia* 63 [Aug.]: 487–492, 7 text figs., pl. 40.

Dendrochiton n. subg.
Mopalia (*Dendrochiton*) *thamnopora* n. sp.

1911f, Dec. 13

Berry, S. S. Note on a new *Abraliopsis* from Japan. *Nautilus* 25(8): 93–94.

Abraliopsis scintillans n. sp.

1912a, Feb. 15

Berry, S. S. Note on the occurrence of a giant squid off the California coast. *Nautilus* 25(10): 117–118.

1912b, May –

Berry, S. S. On a cephalopod new to California with a note on another species. *First Annual Report of Laguna Marine Laboratory*, 83–87, 5 text figs.

1912c, Jul. 24

Berry, S. S. A review of the cephalopods of western North America. *Bulletin of the Bureau of Fisheries* 30(1910): 267–336, 18 text figs., pls. 32–66.

Polypus apollyon n. sp.
Polypus gilbertianus n. sp.
Rossia pacifica diegensis n. subsp.

1912d, Sep. 26

Berry, S. S. A catalogue of Japanese Cephalopoda. *Proceedings of the Academy of Natural Sciences of Philadelphia* 64 [Jul.]: 380–444, 4 text figs., pls. 5–9.

Sepia formosana n. sp.
Octopodoteuthidae n. fam. name
Ommastrephes hawaiiensis n. sp.

1912e, Nov. 8

Berry S. S. Some necessary changes in cephalopod nomenclature. *Science* (N.S.) 36(932): 643–646.

Octopoteuthidae n. fam. name

Benthoteuthidae n. fam. name

1913a, Mar. 4

Berry, S. S. A list of Mollusca from the Musselshell Valley, Montana. *Nautilus* 26(11): 130–131.

1913b, Apr. 4

Berry, S. S. Notes on some West American cephalopods. *Proceedings of the Academy of Natural Sciences of Philadelphia* 65 [Feb.]: 72–77, 2 text figs.

Polypus pricei n. sp.

Calliteuthis (*Meleagroteuthis*) *heteropsis* n. sp.

Gonatus magister n. sp.

1913c, Jun. 4

Berry, S. S. Some new Hawaiian cephalopods. *Proceedings of the United States National Museum* 45(1996): 563–566.

Laetmoteuthis n. gen.

Laetmoteuthis lugubris n. sp.

Scaeurgus patagiatus n. sp.

Euprymna scolopes n. sp.

Teleoteuthis compacta n. sp.

Abralia trigonura n. sp.

Pterygioteuthis microlampas n. sp.

1913d, Aug. –

Berry, S. S. *Nematolampas*, a remarkable new cephalopod from the South Pacific. *Biological Bulletin* 25(3) 208–212, 1 text fig.

Nematolampas n. gen.

Nematolampas regalis n. sp.

1913e, Oct. 21

Berry, S. S. Teuthological Miscellany No. 1. Zoologischer Anzeiger 42(13): 590–592.

Acroteuthis n. gen.

1913f, Dec. 10

Berry, S. S. Another note on Martyn's Universal Conchologist. *Nautilus* 27(8): 95.

1914a, Jun. 13

Berry, S. S. Another giant squid in Monterey Bay. *Nautilus* 28(2): 22–23.

1914b, Jun. 15

Berry, S. S. Notes on a collection of cephalopods from the Kermadec Islands. *Transactions of the New Zealand Institute* 46: 134–149, 4 text figs., pls. 7–10.

Polypus oliveri n. sp.

Polypus (*Pinnoctopus*?) *kermadecensis* n. sp.

Abralia astrolineata n. sp.

Lycoteuthidae n. fam. name.

1914c, Jun. 24

Berry, S. S. The Cephalopoda of the Hawaiian Islands. Bulletin of the *Bureau of Fisheries* 32(1912): 255–362, 40 text figs., pls. 45–55.

Stoloteuthinae n. subfam.

1916a, Jan. 5

Berry, S. S. Three new helices from California. *University of California Publications in Zoology* 16(9): 107–111.

Epiphragmophora petricola n. sp.

Epiphragmophora tudiculata rufiterrae n. subsp.

Polygyra pinicola n. sp.

1916b, Mar. 6

Berry, S. S. Notes on Mollusca of central Montana. *Nautilus* 29(11): 124–128.

1916c, Mar. –

Berry, S. S. The octopod *Ocythoe* in California. *Journal of Entomology and Zoology* 8(1): 1–4, pl. 1.

1916d, Mar. 15

Berry, S. S. Cephalopoda of the Kermadec Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia* 68: 45–66, 22 text figs., pls. 6–9.

Moschites challengeri n. name

Lampadioteuthidae n. fam.

Lampadioteuthis n. gen.

Lampadioteuthis megaleia n. sp.

Eucleoteuthis n. gen.

Megalocranchia pardus n. sp.

Verrilliteuthis n. gen.

1916e, Jun. 5

Berry, S. S. A new ovula from California. *Nautilus* 30(2): 21–22, 1 pl. [pl. 5, fig. 3, *Nautilus* 30(12), May 7, 1917].

Neosimnia catalinensis n. sp.

1916f, Aug. 19

Berry, S. S. Additional records of Mollusca from San Bernardino County, California. *Nautilus* 30(4): 37–39.

1916g, Dec. 4

Berry S. S. San Diego drift shells. *Nautilus* 30(7): 83.

1917a, Mar. 31

Berry, S. S. Cephalopoda. *Scientific Reports of the Australasian Antarctic Expedition 1911–1914*, Series C. 4(2): 1–39, 30 text figs., pls. 10–14.

Stauroteuthis (?) *mawsoni* n. sp.

Moschites albida n. sp.

Moschites adelieana n. sp.

Moschites aurorae n. sp.

Moschites harrissoni n. sp.

1917b, Apr. 6

Berry, S. S. On *Moschites verrucosa* (Verrill) and its allies. *Proceedings of the Academy of Natural Sciences of Philadelphia* 69 [Jan.]: 2–6, 2 text figs., pls. 1–2.

1917c, Apr. –

Berry, S. S. The English sparrow campaign in Redlands. *California Fish and Game* 3(2): 76–77, 1 text fig.

1917d, May –

Berry, S. S. Random notes on the collection and preservation of chitons. *Lorquinia* 1(10): 73–76.

1917e, Jul. 14

Berry, S. S. A new *Sonorella* from Arizona. *Nautilus* 31(1): 14–15.

Sonorella rooseveltiana n. sp.

1917f, Sep. 1

Berry, S. S. Notes on West American chitons—I. 1. Notes on chitons collected by Mr. George Willett in southeastern Alaska. *Proceedings of the California Academy of Sciences* (4)7(10): 229–244, 4 text figs.

Ischnochiton (*Lepidozona*) *willetti* n. sp.

Placiphorella rufa n. sp.

1917g, Sep. 1

Berry, S. S. Notes on West American chitons—I. 2. On the genus *Trachydermon*. *Proceedings of the California Academy of Sciences* (4)7(10): 245–248.

1917h, Dec. 5

Berry, S. S. Chitons taken by the United States Fisheries steamer "Albatross" in the northwest Pacific in 1906. *Proceedings of the United States National Museum* 54(2223): 1–18, 1 text fig., pls. 1–10.

Leptochiton diomedeae n. sp.
Ischnochiton (*Lepidozona*) *amabilis* n. sp.
Ischnochiton (*Lepidozona*) *interfossa* n. sp.
Ischnochiton (*Lepidozona*) *pilsbryanus* n. sp.

1918a, May 5

Berry, S. S. Note on a preoccupied name in Polyplacophora. *Nautilus* 31(4): 144.

Ischnochiton (*Lepidozona*) *nipponica* n. name

1918b, May 18

Berry, S. S. Report on the Cephalopoda obtained by the F.I.S. "Endeavour" in the Great Australian Bight and other southern Australian localities. Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour," 1909–14, 4(5): 201–298, 67 text figs., pls. 59–88.

Enoploteuthis galaxias n. sp.
Calliteuthis miranda n. sp.
Loligo etheridgei n. sp.
Austrorossia n. subgen.
Rossia (*Aust*[*ro*]*rossia*) *australis* n. sp.
Sepia hedleyi n. sp.
Sepia dannevigi n. sp.
Sepia chirotrema n. sp.
Teuthidiscus n. subgen.
Opisthoteuthis pluto n. sp.
Opisthoteuthis persephone n. sp.

1918c, Jul. 20

Berry, S. S. A further note on the genus *Trachydermon*. *Nautilus* 32(1): 12.

Basiliochiton n. name

1919a, Jan. –

Berry, S. S. Preliminary notices of some new West American chitons. *Lorquinia* 2(6): 44–47.

Xiphiozona n. subgen.
Lepidopleurus (*Xiphiozona*) *heathi* n. sp.
Cyanoplax fackenthallae n. sp.
Mopalia egretta n. sp.
Mopalia cirrata n. sp.
Mopalia phorminx n. sp.
Mopalia chacei n. sp.
Placiphorella pacifica n. sp.
Ischnochiton (*Lepidozona*) *asthenes* n. sp.
Ischnochiton (*Lepidozona*) *golischi* n. sp.

1919b, Jun. 16

Berry, S. S. Notes on West American chitons—II. 3. On the generic or subgeneric position of certain West American chitons. *Proceedings of the California Academy of Sciences* (4)9(1): 1–5, 4 text figs.

Tripoplax n. subgen.
Rhombochiton n. subgen.

1919c, Jun. 16

Berry, S. S. Notes on West American chitons—II. 4 New chitons collected by Dr. Harold Heath in Monterey Bay, California. *Proceedings of the California Academy of Sciences* (4)9(1): 6–13, 2 text figs., pls. 1–5.

Hanleya spicata n. sp.

1919d, Jun. 16

Berry, S. S. Notes on West American chitons—II. 5. A new *Mopalia* from southeastern Alaska. *Proceedings of the California Academy of Sciences* (4)9(1): 13–17, pls. 6–7.

1919e, Jun. 16

Berry, S. S. Notes on West American chitons—II. 6. A new *Lepidozona* from southern California. *Proceedings of the California Academy of Sciences* (4)9(1): 18–21, pl. 8.

1919f, Nov. 6

Berry, S. S. Three new alpine vertigos from California. *Nautilus* 33(2): 48–52, 8 text figs.

Vertigo modesta microphasma n. subsp.
Vertigo allyniana n. sp.
Vertigo allyniana xenos n. subsp.

1919g, Dec. 3

Berry, S. S. Mollusca of Glacier National Park, Montana. *Proceedings of the Academy of Natural Sciences of Philadelphia* 71 [Oct.]: 195–205, 1 text fig., pls. 9–10.

Oreohelix cooperi apiarium n. subsp.

1920a, Mar. –

Berry, S. S. Light production is cephalopods, I. An introductory survey. *Biological Bulletin* 38(3): 141–169.

Architeuthoidea n. superfam.
Enoploteuthoidea n. superfam.
Ommastrephoidea n. superfam.
Chiroteuthoidea n. superfam.
Joubiniteuthis n. gen.
Cranchioidea n. superfam.
Loliginoidea n. superfam.
Spiruloidea n. superfam.
Sepioidea n. superfam.
Cirroteuthoidea n. superfam.
Argonautoidea n. superfam.
Amphitretoidea n. superfam.
Polypodoidea n. superfam.

1920b, Apr. 20

Berry, S. S. Turritidae vs. Turridae. *Nautilus* 33(4): 130–133.

1920c, Apr. –

Berry, S. S. Light production in cephalopods, II. An introductory survey. *Biological Bulletin* 38(4): 171–195.

1920d, May 2

Berry, S. S. On *Mitra montereyi*, a new Californian species. *Proceedings of the Malacological Society of London* 14(1): 31–33, 6 text figs.

Mitra montereyi n. sp.

1920e, Aug. 11

Berry, S. S. Notes on some undescribed Californian helices. *Proceedings of the California Academy of Sciences* (4)10(8): 53–70, pls. 4–6.

Epiphragmophora tudiculata allyniana n. subsp.
Epiphragmophora traskii chrysoderma n. subsp.
Epiphragmophora traskii willetti n. subsp.
Epiphragmophora petricola orotes n. subsp.
Epiphragmophora petricola sangabrielis n. subsp.

1920f, Nov. 6

Berry, S. S. Turritidae vs. Turridae. *Nautilus* 34(2): 57–58.

1920g, Nov. 6

Berry, S. S. Note on a preoccupied generic name in cephalopods. *Nautilus* 34(2): 66–67.

Acruroteuthis n. name

1920h, Nov. 10

Berry, S. S. Preliminary diagnoses of new cephalopods from the western Atlantic. *Proceedings of the United States National Museum* 58(2335): 293–300, pl. 16.

Chiroteuthoides n. gen.
Chiroteuthoides hastula n. sp.
Enoptroteuthis n. gen.
Enoptroteuthis spinicauda n. sp.
Ascoteuthis n. subgen.
Teuthowenia (*Ascoteuthis*) *corona* n. sp.
Sandalops pathopsis n. sp.

Sandalops ecthambus n. sp.
Pyrgopsis lemur n. sp.
Polypus scorpio n. sp.

1921a, Jan. 29

Berry, S. S. A review of the cephalopod genera *Sepioloidea, Sepiadarium,* and *Idiosepius. Records of the South Australian Museum* 1(4): 347–364, 4 text figs.

Sepiadarium austrinum n. sp.
Idiosepius notoides n. sp.

1921b, Aug. –

Berry, S. S. A new neotreme brachiopod from California. *Annals and Magazine of Natural History* (9)8: 210–212, pl. 11.

Crania californica n. sp.

1921c, Sep. –

Berry, S. S. Notes on some Japanese cephalopods.—A review of Sasaki's 'Albatross' report. *Annals and Magazine of Natural History* (9)8: 351–353.

Polypus hokkaidensis n. name
Polypus madokai n. name

1921d, Oct. –

Berry, S. S. A distributional note on Haliotis. California Fish and Game 7(4): 254–255, 1 text fig.

1921e, Dec. 5

Berry, S. S. Some land snails of Shasta County, California. *Nautilus* 35(2): 35–39, 1 pl. [pl. 2, figs. 6–9, *Nautilus* 35(3), Jan. 23, 1922].

Polygyra sierrana n. sp.
Polygyra columbiana shasta n. subsp.

1922a, Mar. –

Berry, S. S. Magpies versus livestock: an unfortunate new chapter in avian depredations. *The Condor* 24: 13–17, 2 text figs.

1922b, May 9

Berry, S. S. Land snails from the Canadian Rockies. *Canada Victoria Memorial Museum Bulletin* 36 (Biol. Ser. No. 8): 1–19, pl. 1.

Oreohelix strigosa canadica n. subsp.

1922c, May 16

Berry, S. S. Fossil chitons of western North America. *Proceedings of the California Academy of Sciences* (4)11(18): 399–526, 11 text figs., pls. 1–16.

Leptochiton clarki n. sp.
Oligochiton n. gen.
Oligochiton lioplax n. sp.
Ischnochiton (*Lepidozona*) *sanctaemonicae* n. sp.
Callistochitoninae n. subfam.
Callistochiton decoratus ferminicus n. subsp.

1922d, Jul. 24

Berry, S. S. Localities of northern California land snails: a correction. *Nautilus* 36(1): 32–33.

1922e, Aug. 18

Berry, S. S. Notes on the mollusks of the Colorado Desert,—I. *Proceedings of the Academy of Natural Sciences of Philadelphia* 74: 69–100, 5 text figs., pls. 8–10.

Micrarionta aquae-albae n. sp.
Micrarionta xerophila n. sp.

1923, May, –

Berry, S. S. Observations on a Montana beaver canal. *Journal of Mammalogy* 4(2): 92–103, 1 text fig., pls. 10–11.

1924a, Apr. 24

Berry, S. S. A new zonitid snail from southern California. *Nautilus* 37(4): 130–132, 1 text fig.

Polita gabrielina n. sp.

1924b, Oct. 22

Berry, S. S. [Review of] The life-history and growth of the Pismo clam (*Tivela stultorum* Mawe). By Frank W. Weymouth. *Nautilus* 38(2): 68–71.

1925a, Jun. 1

Berry, S. S. The species of *Basiliochiton. Proceedings of the Academy of Natural Sciences of Philadelphia* 77: 23–29, 2 text figs., pl. 2.

Lophochiton n. subgen.
Basiliochiton lobium n. sp.

1925b, Jul. 11

Berry, S. S. New or little known southern California Lepidozonas. *Proceedings of the Malacological Society of London* 16(5): 228–231, pl. 11.

Ischnochiton (*Lepidozona*) *gallina* n. sp.

1925c, Jul. –

Berry, S. S. On an abnormal specimen of the chiton, *Acanthopleura granulata. Annals and Magazine of Natural History* (9)16: 173–175, 1 text fig., pl. 12.

1925d, Aug. 6

Berry, S. S. The Cephalopoda collected by the Canadian Arctic Expedition, 1913–18. Report of the Canadian Arctic Expedition, 1913–18, 8(B): 1–8, 3 text figs.

1926a, Jan. 11

Berry, S. S. A note on the name *Lophochiton. Nautilus* 39(3): 105.

Ploiochiton n. name

1926b, Oct. –

Berry, S. S. A note on the occurrence and habits of a luminous squid (*Abralia veranyi*) at Madeira. *Biological Bulletin* 51(4): 257–268, 2 text figs.

1926c, Nov. –

Berry, S. S. Fossil chitons from the Pleistocene of San Quintin Bay, Lower California. *American Journal of Science* (5)12: 455–456.

1926d, Nov. –

Berry, S. S. Two new helicoid snails from the Mohave Desert. *Annals and Magazine of Natural History* (9)18: 490–493, 4 text figs.

Helminthoglypta graniticola n. sp.
Helminthoglypta mohaveana n. sp.

1927a, Apr. 29

Berry, S. S. A new Oregonian subspecies of *Monadenia fidelis. Nautilus* 40(4): 122–124, 1 text fig.

Monadenia fidelis celeuthia n. subsp.

1927b, May 27

Berry, S. S. Notes on some British Columbian chitons. *Proceedings of the Malacological Society of London* 17(4): 159–164, 4 text figs., pl. 13.

Dendrochiton semiliratus n. sp.

1928a, Feb. –

Berry, S. S. New helicoid snails from the Mohave Desert.—II. *Annals and Magazine of Natural History* (10)1: 274–279, 8 text figs.

Helminthoglypta jaegeri n. sp.
Helminthoglypta crotalina n. sp.
Helminthoglypta riparia n. sp.

1928b, May –

Berry, S. S. New helicoid snails from the Mohave Desert.—III. *Annals and Magazine of Natural History* (10)1: 618–622, 5 text figs.

Micrarionta (*Eremarionta*) *aetotis* n. sp.
Micrarionta (*Eremarionta*) *depressispira* n. sp.

1928c, Dec. –

Berry, S. S. A new land snail from the Lower California with notes on other species. *Journal of Entomology and Zoology* 20(4): 73–83, 1 text fig., pls. 1–2.

Micrarionta (*Eremarionta*) *inglesiana* n. sp.

1929a, Aug. 5

Berry, S. S. *Loliolopsis chiroctes*, a new genus and species of squid from the Gulf of California. *Transactions of the San Diego Society of Natural History* 5(18): 263–282, 9 text figs., pls. 32–33.

Loliolopsis n. gen
Loliolopsis chiroctes n. sp.

1929b, Oct. 17

Berry, S. S. Three new snails from the hills of California. *Nautilus* 43(2): 39–40.

Micrarionta (*Eremarionta*) *morongoana* n. sp.
Micrarionta (*Eremarionta*) *borregoensis* n. sp.
Helminthoglypta tudiculata kermensis n. subsp. [emended 1930c]

1930a, Jan. 15

Berry, S. S. Snail notes from the California desert. *Nautilus* 43(3): 73–75.

Chamaearionta n. subgen.

1930b, Apr. 24

Berry, S. S. Snails, new and otherwise, from the Palomar Mountains, California. *Nautilus* 43(4): 113–114, 2 text figs.

Vitrea orotis n. sp.

1930c, Apr. 24

Berry, S. S. Three new snails from the hills of California [correction]. *Nautilus* 43(4): 138.

Helminthoglypta tudiculata kernensis [see 1929b]

1930d, Apr. 24

Berry, S. S. Land snails from the San Juan Islands, Washington. *Nautilus* 43(4): 141–142.

1930e, May –

Berry, S. S. Preliminary notices of two new snails from the Colorado Desert. *Annals and Magazine of Natural History* (10)5: 543–545.

Micrarionta (*Eremarionta*) *mille-palmarum* n. sp.
Micrarionta (*Eremarionta*) *callinepius* n. sp.

1930f, Aug. –

Berry, S. S. New helicoid snails from the Mohave Desert.—IV. *Annals and Magazine of Natural History* (10)6: 187–193, 8 text figs.

Micrarionta (*Eremarionta*) *melanopylon* n. sp.
Micrarionta (*Eremarionta*) *micrometalleus* n. sp.
Micrarionta (*Eremarionta*) *avawatzica* n. sp.

1931a, Jan. 27

Berry, S. S. The genus *Oreohelix* in California. *Nautilus* 44(3): 73–75.

1931b, Apr. 27

Berry, S. S. A new Californian race of *Monadenia*. *Nautilus* 44(4): 122–123.

Monadenia fidelis pronotis n. subsp.

1931c, Jul. 15

Berry, S. S. A redescription, under a new name, of a well-known California chiton. *Proceedings of the Malacological Society of London* 19(5): 255–258, pl. 29.

Ischnochiton (*Lepidozona*) *californiensis* n. sp.

1931d, Jul. –

Berry, S. S. New helicoid snails from the Mohave Desert.—V. The genus *Oreohelix* in southern California and Nevada. *Annals and Magazine of Natural History* (10)8: 115–120, 7 text figs.

Oreohelix californica n. sp.
Oreohelix handi jaegeri n. subsp.

1932a, Jan. –

Berry, S. S. Cephalopods of the genera *Sepioloidea, Sepiadarium*, and *Idiosepius*. *Philippine Journal of Science* 47(1): 39–55, pl. 1.

Sepiadarium nipponianum n. sp.

1932b, Dec. –

Berry, S. S. Three new mountain snails from Idaho and Nevada. Journal of *Entomology and Zoology* 24(4): 57–63, 10 text figs.

Oreohelix vortex n. sp.
Oreohelix flammulifer n. sp.
Oreohelix nevadensis n. sp.

1933a, Jun. 16

Berry, S. S. Three new polygyrid snails from California. *Nautilus* 47(1): 12–16, pl. 2.

Polygyra trachypepla n. sp.
Polygyra loricata nortensis n. subsp.
Polygyra hapla n. sp.
Polygyra columbiana oria n. subsp.

1933b, Nov. –

Berry, S. S. Snails and other mollusks, pp. 67–73. In: Jaeger, E. C. *The California Deserts, A Visitor's Handbook*. Stanford University Press.

1934a, Jul. –

Berry, S. S. Class Cephalopoda, pp. 160–165. In: Johnson, C. W. List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proceedings of the Boston Society of Natural History* 40(1): 1–203.

1934b, Aug. –

Berry, S. S. The littoral ark-shells of southern California. [Title only of presented paper] *American Malacological Union Report* 1934: 6.

1935a, Jan 19

Berry, S. S. A further record of a chiton (*Nuttallina*) with nine valves. *Nautilus* 48(3): 89–90, 2 text figs.

1935b, Mar. 30

Berry, S. S. An undescribed Californian *Olivella. Proceedings of the Malacological Society of London* 21(4): 262–265, 1 text fig.

Olivella pycna n. sp.

1936, Nov. –

Berry, S. S. A new *Dimya* from California. *Proceedings of the Malacological Society of London* 22(3): 126–128, pl. 13B.

Dimya californiana n. sp.

1937a, Jan. 29

Berry, S. S. Land snails of Kadiak. *Nautilus* 50(3): 87–88.

1937b, Jul. 3

Berry, S. S. Some lesser races of *Monadenia fidelis* (Gray). *Nautilus* 51(1): 28–33.

Monadenia fidelis ochromphalus n. subsp.
Monadenia fidelis leonina n. subsp.
Monadenia fidelis klamathica n. subsp.

1938a, Mar, –

Berry, S. S. Four new Californian helicoid snails. *Journal of Entomology and Zoology* 30(1): 17–25, 8 text figs.

Helminthoglypta arrosa humboldtica n. subsp.
Helminthoglypta dupetithouarsii consors n. subsp.
Helminthoglypta tejonis n. sp.
Helminthoglypta tudiculata angelena n. subsp.

1938b, Jun. –

Berry, S. S. New helicoid snails from the southern Sierras. *Journal of Entomology and Zoology* 30(2): 41–51, 18 text figs.

Helminthoglypta orina n. sp.
Helminthoglypta isabella n. sp.
Helminthoglypta inglesi n. sp.
Helminthoglypta liodoma n. sp.
Helminthoglypta euomphalodes n. sp.
Helminthoglypta proles saccharodytes n. subsp.
Helminthoglypta napaea n. sp.

Helminthoglypta tularensis pluripuncta n. subsp.

1938c, Jun. –

Berry, S. S. A preliminary revision of the snail-genus *Glyptostoma. Journal of Entomology and Zoology* 30(2): 55–56.

Glyptostoma pilsbryanum n. sp.

Glyptostoma pilsbryanum binneyanum n. subsp.

1939, Oct. 20

Berry, S. S. Two new polygyroid helicoids from northern California. *Nautilus* 53(2): 56–61, 1 text fig.

Mesodon (*megasoma*, subsp. ?) *eritrichius* nov. [race]

Mesodon (*megasoma*, subsp. ?) *euthales* nov. [race]

1940a, Feb. 10

Berry, S. S. A proposed dichotomy of the snail-genus *Monadenia. Bulletin of Southern California Academy of Sciences* 38(3): 203–205.

Corynadenia n. subgen.

1940b, Mar. –

Berry, S. S. Nine new snails of the genus *Monadenia. Journal of Entomology and Zoology* 32(1): 1–17, 18 text figs.

Monadenia marmarotis n. sp.

Monadenia rotifer n. sp.

Monadenia callipeplus n. sp.

Monadenia cristulata n. sp.

Monadenia chaceana n. sp.

Monadenia fidelis scottiana n. subsp.

Monadenia fidelis callidina n. subsp.

Monadenia fidelis smithiana n. subsp.

Monadenia infumata alamedensis n. subsp.

1940c, Sep. 28

Berry, S. S. New Mollusca from the Pleistocene of San Pedro, California—I. *Bulletins of American Paleontology* 25(94A): 147–164, pls. 17–18 [separates numbered: 1–18, pls. 1–2].

Crassinella nuculiformis n. sp.

Tivela scarificata n. sp.

Clavus (*Crasispira*) *zizyphus* n. sp.

Verticumbo n. gen.

Verticumbo charybdis n. sp.

Acmaea lepisma n. sp.

Astraea (*Pomaulax*) *petrothauma* n. sp.

Calliostoma grantianum n. sp.

1941, Oct. 7

Berry, S. S. New Mollusca from the Pleistocene of San Pedro, California—II. *Bulletins of American Paleontology* 27(101): 1–18, pl. 1 [separates numbered: 1–18, pl. 1].

Actaeon (*Microglyphis*) *schencki* n. sp.

Oenopota turrispira n. sp.

Moniliopsis chacei n. sp.

Clathurella (*Glyphostoma*) *tridesmia* n. sp.

Mitromorpha barbarensis woodfordi n. subsp.

Mitromorpha galeana n. sp.

Margarites (*Lirularia*) *aresta* n. sp.

Skenea (?) *cyclostoma* n. sp.

1943, Dec. 30

Berry, S. S. On the generic relationships of certain Californian xerophile snails. *Transactions of the San Diego Society of Natural History* 10(1): 1–24, 8 text figs., pls. 1–2.

Mohavelix n. subgen.

Sonorelix n. gen.

1944, May 4

Berry, S. S. A second Californian *Dimya. Proceedings of the Malacological Society of London* 26(1): 25–26, 4 text figs.

Dimya coralliotis n. sp.

1945a, Sep. –

Berry, S. S. Two new chitons from the Gulf of California. *American Midland Naturalist* 34(2): 491–495, 18 text figs.

Chaetopleura (*Pallochiton*) *euryplax* n. sp.

Stenoplax histrio n. sp.

1945b, Dec. 17

Berry, S. S. Chitons, their collection and preservation. *Mollusca,* [Tavares, Florida], 1(7): 89–94, 99–102.

1946, Jan. 31

Berry, S. S. A re-examination of the chiton, *Stenoplax magdalenensis* (Hinds), with description of a new species. *Proceedings of the Malacological Society of London* 26(6): 161–166, 6 text figs., pls. 4–5.

Stenoplax (*Stenoradsia*) *heathiana* n. sp.

1946b, May 8

Berry, S. S. A new Californian *Neosimnia. Journal of Conchology* 22(8): 190–193, 4 text figs.

Neosimnia bella-maris n. sp.

1946c, Oct. –

Berry, S. S. A shell necklace from the Havasupai Indians. *Plateau* 19(2): 29–34, 2 text figs.

1946d, Nov. 4

Berry, S. S. Californian forms of *Pedicularia. Leaflets in Malacology* 1(1): 1–4, 3 text figs.

Pedicularia (*californica* phase or form?) *ovuliformis* nov.

1947a, Jan. 11

Berry, S. S. A new *Pyrgulopsis* from Oregon. *Nautilus* 60(3): 76–78, pl. 7.

Pyrgulopsis archimedis n. sp.

1947b, May 3

Berry, S. S. A surprising molluscan discovery in Death Valley. *Leaflets in Malacology* 1(2): 5–8, 2 text figs.

Assiminea infima n. sp.

1947c, Oct. 1

Berry, S. S. On the generic relationships of certain Lower Californian helicoid snails. *Leaflets in Malacology* 1(3): 9–12.

Herpeteros n. subgen.

1947d, Nov. 14

Berry, S. S. New Mollusca from the Pleistocene of San Pedro, California—III. *Bulletins of American Paleontology* 31(127): 255–274, pls. 26–27 [separates numbered: 1–20, pls. 1–2].

Nucula (*Ennucula*) *microsperma* n. sp.

Adontorhina n. gen.

Adontorhina cyclia n. sp.

Antiplanes macfarlandi n. sp.

Mistostigma n. gen.

Mistostigma punctulum n. sp.

Puncturella punctocostata n. sp.

Puncturella ralphi n. sp.

Scissurella lyra n. sp.

1948a, Jan. –

Berry, S. S. Snails of the Sierra Ancha, Arizona. *American Midland Naturalist* 39(1): 151–159, 16 text figs.

Sonorella strongiana n. sp.

Sonorella anchana n. sp.

1948b, Feb. 20

Berry, S. S. Two misunderstood west American chitons. *Leaflets in Malacology* 1(4): 13–15.

Lepidochitona keepiana n. sp.

1948c, Feb. 20

Berry, S. S. A note on Rowell's types in *Pupa* and *Gundlachia. Leaflets in Malacology* 1(4): 16.

1948d, Mar. –

Berry, S. S. On *Opalia montereyensis* (Dall). *Journal of Entomology and Zoology* 40(1): 15–19, 5 text figs.

1948e, May –

Berry, S. S. A noteworthy molluscan faunule from northeastern Washington. *American Midland Naturalist* 39(3): 721–727, 1 text fig.

1949a, Jun. 13

Berry, S. S. A new *Opisthoteuthis* from the eastern Pacific. *Leaflets in Malacology* 1(6): 23–26.

Opisthoteuthis californiana n. sp.

1949b, —

Berry, S. S. A survey and natural history of *Argonauta* [Title only of presented paper] *American Malacological Union News Bulletin and Annual Report*, 1948 [Bull. No. 15]: 22.

1949c, —

Berry, S. S. The holotype of *Murex petri*, Dall. (Abstract) *American Malacological Union News Bulletin and Annual Report*, 1948 [Bull. No. 15]: 24.

1950a, —

Berry, S. S. A new spectacular find—a new cephalopod found in California. [Title only of presented paper] *American Malacological Union News Bulletin and Annual Report*, 1949 [Bull. No. 16]: 19.

1950b, —

Berry, S. S. New light on the taxonomy of west American species of *Crepidula*. (Abstract) *American Malacological Union News Bulletin and Annual Report*, 1949 [Bull. No. 16]: 22.

1950c, Nov. 14

Berry, S. S. A partial review of some west American species of Crepidula. Leaflets in Malacology 1(8): 35–40.

Crepidula coei n. sp.

1950d, Nov. 14

Berry, S. S. A pteropod new to California. *Leaflets in Malacology* 1(8): 41–42.

1951, Jun. 8

Berry, S. S. Notes on some British Columbian chitons.—II. *Proceedings of the Malacological Society of London* 28(6): 213–229, 14 text figs., pls. 26–27.

Mopalia cithara n. sp.

1952a, Apr. –

Berry, S. S. The flapjack devilfish, *Opisthoteuthis*, in California. *California Fish and Game*, 38(2): 183–188, 5 text figs.

1952b, Jul. 10

Berry, S. S. Another interesting addition to the Californian pteropod fauna. *Leaflets in Malacology* 1(9): 50.

1953a, Apr. 17

Berry, S. S. Two Californian mountain snails of the genus *Helminthoglypta*—a problem in the relationship of species. *Transactions of the San Diego Society of Natural History* 11(12): 329–344, 4 text figs., pls. 24–25.

Helminthoglypta thermimontis n. sp.

1953b, Aug. 14

Berry, S. S. West American razor-clams of the genus *Ensis. Transactions of the San Diego Society of Natural History* 11(15): 393–404, 4 text figs. and 11(16): pl. 29, Sep. 1, 1953.

Ensis myrae n. sp.

1953c, Sep. 1

Berry, S. S. Notices of new West American marine Mollusca. *Transactions of the San Diego Society of Natural History* 11(16): 405–428, 10 figs., pls. 28–29.

Volsella sacculifer n. sp.
Diplodonta impolita n. sp.
Lacuna succinea n. sp.
Turritella orthosymmetra n. sp.
Ocenebra crispatissima n. sp.
Nassarius (*Schizopyga*) *rhinetes* n. sp.
Agaronia murrha n. sp.
Antiplanes (*Ractiplanes*) *willetti* n. sp.
Knefastia princeps n. sp.
Woodbridgea n. gen.
Woodbridgea williamsi n. sp.
Micraenigma n. gen.
Micraenigma oxystoma n. sp.

1953d, Sep. –

Berry, S. S. Molluscan notes from the Puerto Penasco region, Sonora. (Abstract) Minutes of the Conchological Club of Southern California, 131: 3.

1953e, Dec. 18

Berry, S. S. Preliminary diagnoses of six west American species of *Octopus*. *Leaflets in Malacology* 1(10): 51–58.

Octopus rubescens n. sp.
Octopus micropyrsus n. sp.
Octopus hubbsorum n. sp.
Octopus fitchi n. sp.
Octopus alecto n. sp.
Octopus veligero n. sp.

1953f, Dec. 31

Berry, S. S. A quart of Sonoran sand. (Abstract) *Annual Report of the American Malacological Union*, 1953 [Bull. No. 20]: 21.

1953g, Dec. 31

Berry, S. S. A terrestrial molluscan faunule from the Miocene of Montana. (Abstract) *Annual Report of the American Malacological Union*, 1953 [Bull. No. 20]: 23.

1953h, Dec. 31

Berry, S. S. On the supposed stenobathic habitat of the California mussel. (Abstract) *Annual Report of the American Malacological Union*, 1953 [Bull. No. 20]: 27–28.

1953i, Dec. 31

Berry, S. S. The male flapjack devilfish. (Abstract) *Annual Report of the American Malacological Union*, 1953 [Bull. No. 20]: 29.

1954a, Jan. –

Berry, S. S. On the supposed stenobathic habitat of the California sea-mussel. *California Fish and Game*, 40(1): 69–73, 1 text fig.

1954b, Jan. 28

Berry, S. S. and B. W. Halstead *Octopus* bites—a second report. *Leaflets in Malacology* 1(11): 59–65, 1 text fig.

1954c, Jan. 28

Berry, S. S. *Octopus penicillifer*, new species. *Leaflets in Malacology* 1(11): 66.

Octopus penicillifer n. sp.

1954d, Jul. 1

Berry, S. S. West American molluscan miscellany.—I. 1. An hitherto unnamed West American ark-shell. *Leaflets in Malacology* 1(12): 67–70.

Barbatia (*Acar*) *rostae* n. sp.

1954e, Jul. 1

Berry, S. S. West American molluscan miscellany.—I. 2. A new genus of Fissurellidae. *Leaflets in Malacology*, 1(12): 70.

Stromboli n. gen.

1954f, Jul. 7

Berry, S. S. New Californian Pleistocene Eulimidae. *Bulletins of American Paleontology* 35(151): 255–270, pl. 1.

Balcis (*Balcis*) *clavella* n. sp.
Balcis (*Balcis*) *tersa* n. sp.
Balcis (*Vitreolina*) *obstipa* n. sp.

Balcis (*Vitreolina*) *incallida* n. sp.
Balcis (*Vitreolina*) *ebriconus* n. sp.

1954g, Dec. –

Berry, S. S. and C. L. Hubbs. The distribution, past and present, of *Cryptochiton*. (Abstract) *American Malacological Union Annual Report*, 1954 [Bull. No. 21]: 22.

1954h, Dec. –

Berry, S. S. Importance of the large pyramidellid elements in the West American fauna. (Abstract) *American Malacological Union Annual Report*, 1954 [Bull. No. 21]: 25.

1955a, Apr. –

Berry, S. S. On recent Californian occurrences of the rare octopod *Ocythoe*. *California Fish and Game* 41(2): 177–181, 1 text fig.

1955b, May 4

Berry, S. S. A new Sierran pulmonate of the genus *Monadenia*. *Bulletin of the Southern California Academy of Sciences* 54(1): 14–16, pl. 6.

Monadenia (*Corynadenia*) *tuolumneana* n. sp.

1955c, May 4

Berry, S. S. An important new land-snail from the Mission Range, Montana. *Bulletin of the Southern California Academy of Sciences* 54(1): 17–19, pls. 7–8.

Discus (*Gonyodiscus* ?) *brunsoni* n. sp.

1955d, Jul. –

Berry, S. S. The male flapjack devilfish. *California Fish and Game* 41(3): 219–224, 4 text figs.

1955e, —

Berry, S. S. Comment on generic name *Acmaea* Eschscholtz, 1833 vs. *Acmea* Hartmann, 1821. Opinion 344, in Opinions and Declarations rendered by the International Commission on Zoological Nomenclature, 10(1): 338.

1955f, —

Berry, S. S. Chitons, their collection and preservation. In: *How to Collect Shells* (*A Symposium*), pp. 26–32. Published by the American Malacological Union, 26–32. [Partial reprint from Mollusca, 1(7): 89–94, 1945.]

1955g, Dec. 31

Berry, S. S. The West coast's confused and confusing white slipper shells, *Crepidula*, subgenus *Ianacus*. (Abstract) *American Malacological Union Bulletin*, 22: 32.

1956a, Feb. 20

Berry, S. S. A tidal flat on the Vermilion Sea. *Journal of Conchology* 24(3): 81–84.

1956b, May –

Berry, S. S. Mollusca dredged by the *Orca* off the Santa Barbara Islands, California, in 1951. *Journal of the Washington Academy of Sciences* 46(5): 150–157, 9 text figs.

Balcis (*Vitreolina*) *titubans* n. sp.
Admete seftoni n. sp.
Pseudomelatoma sticta n. sp.

1956c, Jul. 9

Berry, S. S. Diagnoses of new eastern Pacific chitons. *Leaflets in Malacology* 1(13): 71–74.

Nuttallina crossota n. sp.
Stenoplax circumsenta n. sp.
Stenoplax isoglypta n. sp.
Stenoplax (*Maugerella*) *conspicua sonorana* n. subsp.
Lepidozona subtilis n. sp.

1956d, Oct. –

Berry, S. S. A new West Mexican prosobranch mollusk parasitic on echinoids. *American Midland Naturalist* 56(2): 355–357, 2 text figs.

Turveria n. gen.
Turveria encopendema n. sp.

1956e, Dec. 31

[Comments on various presented papers]. *American Malacological Union Bulletin*, 23: 6, 11, 14, 16, 17.

1957, Jul. 19

Berry, S. S. Notices of new eastern Pacific Mollusca.—I. *Leaflets in Malacology* 1(14): 75–82.

Pecten (*Leptopecten*) *euterpes* n. sp.
Lithophaga (*Labis*) *attenuata rogersi* n. subsp.
"*Acmaea*" *stanfordiana* n. sp.
Astraea guadalupeana n. sp.
Turritella anactor n. sp.
Acanthina tyrianthina n. sp.
Hanetia macrospira n. sp.
Hanetia capitanea n. sp.
Mitra semiusta n. sp.
Pleuroliria parthenia n. sp.
Pleuroliria artia n. sp.

1958a, Jan. 1

Berry, S. S. Is the Colorado River an efficient barrier to mollusk distribution? (Abstract) *American Malacological Union Bulletin*, 24: 24.

1958b, Jan. 1

Berry, S. S. Double-trouble in violet snails. (Abstract) *American Malacological Union Bulletin*, 24: 27.

1958c, Mar. 28

Berry, S. S. Notices of new eastern Pacific Mollusca.—II. *Leaflets in Malacology* 1(15): 83–90.

Tiphyocerma n. gen.
Tiphyocerma preposterum n. sp.
Muricanthus callidinus n. sp.
Olivella (*Olivella*) *fletcherae* n. sp.
Olivella (*Macgintiella*) *walkeri* n. sp.
Gemmula hindsiana n. sp.
Tiariturris n. gen.
Tiariturris spectabilis n. sp.
Knefastia walkeri n. sp.
Turrigemma n. gen.
Turrigemma torquifer n. sp.
Terebra (*Strioterebrum*) *fitchi* n. sp.
Hormospira n. gen.

1958d, May 31

Berry, S. S. West American molluscan miscellany.—II. 1. Proposal of five new generic taxons. *Leaflets in Malacology* 1(16): 91–95.

Nomaeopelta n. gen.
Stearnsium n. gen.
Lapsigyrus n. gen.
Opeatostoma n. gen.
Mitromica n. gen.

1958e, May 31

Berry, S. S. West American molluscan miscellany.—II. 2. A puzzling new prosobranchiate gastropod. *Leaflets in Malacology* 1(16): 95–96.

Hertleinella n. gen.
Hertleinella leucostephes n. sp.

1958f, May 31

Berry, S. S. West American molluscan miscellany.—II. 3. A redescription of the common Californian *Terebra*. *Leaflets in Malacology* 1(16): 96–98.

Terebra (*Strioterebrum*) *danai* n. sp.

1959a, Jan 1

Berry, S. S. Notes on the natural history of *Nomaeopelta*, a remarkable genus of limpets. [Title only of presented paper] *American Malacological Union Bulletin*, 25: 36.

1959b, Jan. 1

Berry, S. S. *Tiphyocerma*, a strange gastropod. (Abstract) *American Malacological Union Bulletin*, 25: 40.

1959c, Jul. 29

Berry, S. S. Comments on some of the trivaricate muricines. *Leaflets in Malacology* 1(17): 106 and 1(18): 113–114.

Calcitrapessa n. gen.

1959d, Jul. 29

Berry, S. S. Notices of some eastern Pacific Mollusca.—III. *Leaflets in Malacology* 1(18): 107–113.

Botula cylista n. sp.

Spondylus ursipes n. sp.

Galeomma (*Lepirodes* ?) *mexicanum* n. sp.

Diodora pusilla n. sp.

Lucapinella milleri n. sp.

Nomaeopelta myrae n. sp.

Bessomia n. subgen.

Thyca (*Bessomia*) *callista* n. sp.

Cantharus shaskyi n. sp.

Hanetia mendozana n. sp.

Terebra (*Strioterebrum*) *puncturosa* n. sp.

1960a, Jan. 1

Berry, S. S. Some recent finds of interest in west Mexico Mollusca. (Abstract) *American Malacological Union Bulletin* 26: 33.

1960b, Jan. 1

Berry, S. S. Random notes on the biota of the San Bernardino Mountains. (Abstract) *American Malacological Union Bulletin* 26: 42.

1960c, Jan. 1

Berry, S. S. The nature and relationship of the Panamic fauna as manifested by the Mollusca. (Abstract) *American Malacological Union Bulletin* 26: 44–45.

1960d, Dec. 31

Berry, S. S. Notices of new eastern Pacific Mollusca.—IV. *Leaflets in Malacology* 1(19): 115–122.

Pegmapex n. gen.

Pegmapex phoebe n. sp.

Pitar (*Lamelliconcha*) *hesperius* n. sp.

Mactra (*Mactra*) *williamsi* n. sp.

"*Acmaea*" *acutapex* n. sp.

"*Acmaea*" *goodmani* n. sp.

"*Acmaea*" *gabatella* n. sp.

Neosimnia vidleri tyrianthina n. subsp.

Bursa californica sonorana n. subsp.

Murex (*Murex*) *tricoronis* n. sp.

Coralliophila incompta n. sp.

Mitra (*Tiara*) *directa* n. sp.

Mitra (*Tiara*) *calodinota* n. sp.

Mitra (*Tiara*) *lindsayi* n. sp.

1961a, Jan. 1

Berry, S. S. Monograph on the species of the genus Thyca. [Title only of presented paper] *American Malacological Union Bulletin*, 27: 42.

1961b, —

Berry, S. S. Amphineura. In: *The Encyclopedia of the Biological Sciences*, Peter Gray ed., p. 25–26, Reinhold Publishing, New York, 1961.

1961c, Aug. –

Berry, S. S. [Review of] *Carribean Seashells*. By G. L. Warmke and R. T. Abbott. Shells and their Neighbors, 6: 6.

1962, Nov. 13

Berry, S. S. A note on *Cantharus*, with proposal of a new specific name. *Leaflets in Malacology* 1(20): 129–130.

Cantharus rehderi n. name

1963a, Feb. 5

Berry, S. S. Additional comment on *Cionella* and *Vallonia* in California. *Leaflets in Malacology* 1(21): 134.

1963b, Mar. 29

Berry, S. S. Diagnoses of new eastern Pacific chitons—II. *Leaflets in Malacology* 1(22): 135–138.

Dendrochiton psaltes n. sp.

Dendrochiton laurae n. sp.

Dendrochiton lirulatus n. sp.

Lepidozona pella n. sp.

Lepidozona inefficax n. sp.

1963c, Jul. –

Berry, S. S. A "Doratopsis" larva of the squid family Chiroteuthidae in Californian waters. *California Fish and Game* 49(3): 128–139, 6 text figs.

1963d, Sep. 30

Berry, S. S. Notices of new eastern Pacific Mollusca.—V. *Leaflets in Malacology* 1(23): 139–146.

Pecten lunaris n. sp.

Tellidorella n. gen.

Tellidorella cristulata n. sp.

Crenimargo n. gen.

Crenimargo electilis n. sp.

Transennella caryonautes n. sp.

"*Acmaea*" *concreta* n. sp.

Cirsotrema pentedesmium n. sp.

Crucibulum castellum n. sp.

Crucibulum subactum n. sp.

Solenosteira gatesi n. sp.

Olivella (*Dactylidella*) *cymatilis* n. sp.

1964a, Jul. 29

Berry, S. S. Notices of new eastern Pacific Mollusca.—VI. *Leaflets in Malacology* 1(24): 147–154.

Rimula californiana n. sp.

Lunaia n. gen.

Lunaia lunaris n. sp.

Trialatella n. gen.

Trialatella cunninghamae n. sp.

Diptychophlia n. gen.

Pseudomelampus mexicanus n. sp.

Melampus mousleyi n. sp.

Melampus olivaceus californianus n. subsp.

Cymatioa n. name

1964b, Dec. 1

Berry, S. S. Notes on new tropical American records. (Abstract) *American Malacological Union Bulletin* 31: 47.

1965, Dec. 1

Berry, S. S. Good molluscan bibliographies—few and far between. (Abstract) *American Malacological Union Bulletin* 32: 53–55.

1968a, Mar. 20

Berry, S. S. A few rare books. (Abstract) *American Malacological Union Bulletin* 34: 69–71.

1968b, Mar. 20

Berry, S. S. Some unusual mollusks, mainly Panamic. (Abstract) *American Malacological Union Bulletin* 34: 71–72.

1968c, Sep. 26

Berry, S. S. Notices of new eastern Pacific Mollusca.—VII. *Leaflets in Malacology* 1(25): 155–158.

Aequipecten (*Leptopecten*) *camerella* n. sp.
Pteropurpura (*Centrifuga*) *deroyana* n. sp.
Conus poormani n. sp.
Conus chrysocestus n. sp.
Ptychosyrinx chilensis n. sp.

1969, Dec. 17

Berry, S. S. Notices of new eastern Pacific Mollusca.—VIII. *Leaflets in Malacology* 1(26): 159–166.

Rimula mexicana n. sp.
Turcica admirabilis n. sp.
Crucibulum cyclopium n. sp.
Crucibulum monticulus n. sp.
Acanthotrophon sentus n. sp.
Mitra (*Subcancilla*) *phorminx* n. sp.
Oliva ionopsis n. sp.
Elaeocyma ricaudae n. sp.
Elaeocyma baileyi n. sp.
Siphonaria williamsi n. sp.

1974, Nov. 12

Berry, S. S. In: Keen, A.M. Excerpts from and comments on: "Stanford contributions to malacology—an evaluation and appreciation" by S. Stillman Berry. [Originally presented as banquet address to the meeting of the American Malacological Union, Pacific Division at Stanford, July 15, 1955]. *Western Society of Malacologists Annual Report* 7: 18–19.

1975, Nov. 1

Berry, S. S. Remarks on *Ocythoe*. [Title only of presented paper] *Western Society of Malacologists Annual Report* 8: 10.

ALPHABETICAL LIST OF THE NEW TAXA PROPOSED BY S. STILLMAN BERRY

Acroteuthis 1913e
Acruroteuthis 1920g
acutapex, Acmaea 1960d
adelieana, Moschites 1917a
admirabilis, Turcica 1969
Adontorhina 1947d
aetotis, Micrarionta (Eremarionta) 1928b
alamedensis, Monadenia infumata 1940b
alba, Murex carpenteri 1908a
albida, Moschites 1917a
alecto, Octopus 1953e
allyniana, Epiphragmophora tudiculata 1920e
allyniana, Vertigo 1919f
amabilis, Ischnochiton (Lepidozona) 1917h
Amphitretoidea 1920a
anactor, Turritella 1957
anchana, Sonorella 1948a
angelena, Helminthoglypta tudiculata 1938a
apiarium, Oreohelix cooperi 1919g
apollyon, Polypus 1912c
aquae-albae, Micrarionta 1922e
archimedis, Pyrgulopsis 1947a
Architeuthoidea 1920a
aresta, Margarites (Lirularia) 1941
Argonautoidea 1920a
artia, Pleuroliria 1957
(Ascoteuthis), Teuthowenia 1920h
asthenes, Ischnochiton (Lepidozona) 1919a
astrolineata, Abralia 1914b
astrosticta, Abralia 1909b
aurorae, Moschites 1917a
australis, Rossia (*Aust*[ro]rossia) 1918b
austrinum, Sepiadarium 1921a
(Austrorossia), Rossia 1918b
avawatzica, Micrarionta (Eremarionta) 1930f
baileyi, Elaeocyma 1969
Basilochiton 1918c
bella-maris, Neosimnia 1964b
Benthoteuthidae 1912e
(Bessomia), Thyca 1959d
bifasciata, Nassa perpinquis 1908c
binneyanum, Glyptosoma pilsbryanum 1938c
borregoensis, Micrarionta (Eremarionta) 1929b
brunsoni, Discus (Gonyodiscus?) 1955c
Calcitrapessa 1959c
californiana, Dimya 1936
californiana, Opisthoteuthis 1949a
californiana, Rimula 1964a
californianus, Melampus olivaceus 1964a
californica, Crania 1921b
californica, Oreohelix 1931d
californicus, Polypus 1911c
californiensis, Ischnochiton (Lepidozona) 1931c
callidina, Monadenia fidelis 1940b
callidinus, Muricanthus 1958c
callinepius, Micrarionta (Eremarionta) 1930e
callipeplus, Monadenia 1940b
callista, Thyca (Bessomia) 1959d
Callistochitoninae 1922c
calodinota, Mitra (Tiara) 1960d
camerella, Aequipecten (Leptopecten) 1968c
canadica, Oreohelix strigosa 1922b
capitanea, Hanetia 1957
caryonautes, Transennella 1963d
castellum, Crucibulum 1963d
catalinensis, Neosimnia 1916e
celeuthia, Monadenia fidelis 1927a
chaceana, Monadenia 1940b
chacei, Moniliopsis 1941
chacei, Mopalia 1919a
challengeri, Moschites 1916d
(Chamaearionta), Micrarionta 1930a
charybdis, Verticumbo 1940c
chilensis, Ptychosyrinx 1968c
chiroctes, Loliolopsis 1929a
Chiroteuthoidea 1920a
Chiroteuthoides 1920h
chirotrema, Sepia 1918b
chrysocestus, Conus 1968c
chrysoderma, Epiphragmophora traskii 1920e
circumsenta, Stenoplax 1956c
cirrata, Mopalia 1919a
Cirroteuthoidea 1920a
cithara, Mopalia 1951
clarki, Leptochiton 1922c
clavella, Balcis (Balcis) 1954f
coei, Crepidula 1950c
compacta, Teleoteuthis 1913c
concreta, Acmaea 1963d
consors, Helminthoglypta dupetithouarsii 1938a
coralliotis, Dimya 1944
corona, Teuthowenia (Ascoteuthis) 1920h
(Corynadenia), Monadenia 1940a
Cranchioidea 1920a
Crenimargo 1963d
crispatissima, Ocenebra 1953c
cristulata, Monadenia 1940b
cristulata, Telliodorella 1963d
crossota, Nuttalina 1956c
crotalina, Helminthoglypta 1928a
cunninghamae, Trialatella 1964a
cyclia, Adontorhina 1947d
cyclopium, Crucibulum 1969

cyclostoma, Skenea (?) 1941
cylista, Botula 1959d
cymatilis, Olivella (Dactylidella) 1963d
Cymatioa 1964a
danai, terebra (Striaterebrum) 1958f
dannevigi, Sepia 1918b
(Dendrochiton), Mopalia 1911e
depressispira, Micrarionta (Eremarionta) 1928b
deroyana, Pteropurpura (Centrifuga) 1968c
diegensis, Rossia pacifica 1912c
diomedeae, Leptochiton 1917h
Diptychophilia 1964a
directa, Mitra (Tiara) 1960d
ebriconus, Balcis (Vitreolina) 1954f
echthambus, Sandalops 1920h
egretta, Mopalia 1919a
electilis, Crenimargo 1963d
encopendema, Turveria 1956d
Enoploteuthoidea 1920a
Enoptroteuthis 1920h
eritrichius, Mesodon (megasoma, subsp.?) 1939
etheridgei, Loligo 1918b
Eucleoteuthis 1916d
euomphalodes, Helminthoglypta 1938b
euryplax, Chaetopleura (Pallochiton) 1945a
euterpes, Pecten (Leptopecten) 1957
euthales, Mesodon (megasoma, subsp.?) 1939
fackenthallae, Cyanoplax 1919a
famelica, Chiroteuthis 1909b
ferminicus, Callistochiton decoratus 1922c
fisheri, Helicocranchia 1909b
fitchi, Octopus 1953e
fitchi, Terebra (Strioterebrum) 1958c
flammulifer, Oreohelix 1932b
fletcherae, Olivella (Olivella) 1958c
formosana, Sepia 1912d
gabatella, Acmaea 1960d
gabrielina, Polita 1924a
galaxias, Enoploteuthis 1918b
galeana, Mitromorpha 1941
gallina, Ischnochiton (Lepidozona) 1925b
gatesi, Solenostiera 1963d
gilbertianus, Polypus 1912c
globula, Cranchia (Liocranchia) 1909b
golischi, Ischnochiton (Lepidozona) 1919a
goodmani, Acmaea 1960d
grantianum, Calliostoma 1940c
granticola, Helminthoglypta 1926d
guadalupeana, Astraea 1957
hapla, Polygyra 1933a
harrissoni, Moschites 1917a
hastula, Chiroteuthoides 1920h
hawaiiensis, Ommastrephes 1912d
hawaiiensis, Stephanoteuthis 1909b
heathi, Eledonella 1911c
heathi, Lepidopleurus (Xiphiozona) 1919a
heathiana, Stenoplax (Stenoradsia) 1946a
hedleyi, Sepia 1918b
(Herpeteros), Sonorelix 1947c
Hertleinella 1958e
hesperius, Pitar (Lamelliconcha) 1960d
heteropsis, Calliteuthis (Meleagroteuthis) 1913b
hindsiana, Gemmula 1958c
histrio, Stenoplax 1945a
hokkaidensis, Polypus 1921c
Hormospira 1958c
hoylei, Polypus 1909b
hubbsorum, Octopus 1953e
humboldtica, Helminthoglypta arrosa 1938a
hyporhyssa, Cerithidea sacrata 1906
impolita, Diplodonta 1953c
incallida, Balcis (Vitreolina) 1954f
incompta, Coralliophila 1960d
inefficax, Lepidozona 1963b
infima, Assiminea 1947b
inglesi, Helminthoglypta 1938b
inglesiana, Micrarionta (Eremarionta) 1928c
interfossa, Ischnochiton (Lepidozona) 1917h
ionopsis, Oliva 1969
iris, Stoloteuthis 1909b
isabella, Helminthoglypta 1938b
isoglypta, Stenoplax 1956c
jaegeri, Helminthoglypta 1928a
jaegeri, Oreohelix handi 1931d
Joubiniteuthis 1920a
keepiana, Lepidochitona 1948b
kermadecensis, Polypus (Pinnoctopus?) 1941b
kernensis, Helminthoglypta tudiculata 1930c
klamathica, Monodenia fidelis 1937b
Laetmoteuthis 1913c
Lampadioteuthidae 1916d
Lampadioteuthis 1916d
Lapsigyrus 1958d
laurae, Dendrochiton 1963b
leioderma, Polypus 1911c
lemur, Pyrgopsis 1920h
leonina, Monodenia fidelis 1937b
lepisma, Acmaea 1940c
leucostephes, Hertleinella 1958e
lindsayi, Mitra (Tiara) 1960d
liodoma, Helminthoglypta 1938b
lioplax, Oligochiton 1922c
lirulatus, Dendrochiton 1963b
lobium, Basiliochiton 1925a
Loliginoidea 1920a
Loliolopsis 1929a
(Lophochiton), Basiliochiton 1925a
lugubris, Laetmoteuthis 1913c
Lunaia 1964a
lunaris, Lunaia 1964a
lunaris, Pecten 1963d
Lycoteuthidae 1914b
lyra, Scissurella 1947d
macfarlandi, Antiplanes 1947d
macrope, Cirroteuthis 1911c
macrospira, Hanetia 1957
madokai, Polypus 1921c
magister, Gonatus 1913b
marmarotis, Monadenia 1940b
mawsoni, Stauroteuthis (?) 1917a
megaleia, Lampadioteuthis 1916d

melanopylon, Micrarionta (Eremarionta) 1930f
mendozana, Hanetia 1959d
mexicana, Rimula 1969
mexicanum, Galeomma (Lepirodes?) 1959d
mexicanus, Pseudomelampus 1964a
Micraenigma 1953c
microlampas, Pterygioteuthis 1913c
micrometalleus, Micrarionta (Eremarionta) 1930f
microphasma, Vertigo modesta 1919f
micropyrsus, Octopus 1953e
microsperma, Nucula (Ennucula) 1947d
*mille-palmarum, Micrarionta (Eremarionta)*1930e
milleri, Lucapinella 1959d
miranda, Calliteuthis 1918b
Mistostigma 1947d
Mitromica 1958d
mohaveana, Helminthoglypta 1926d
(Mohavelix), Sonorella 1943
montereyi, Mitra 1920d
monticulus, Crucibulum 1969
morongoana, Micrarionta (Eremarionta) 1929b
mousleyi, Melampus 1964a
murrha, Agaronia 1953c
myrae, Ensis 1953b
myrae, Nomaeopelta 1959d
napaea, Helminthoglypta 1938b
Nematolampas 1913d
nevadensis, Oreohelix 1932b
nipponensis, Stoloteuthis 1911a
nipponianum, Sepiadarium 1932a
nipponica, Ischnochiton (Lepidozona) 1918a
Nomaeopelta 1958d
nortensis, Polygyra loricata 1933a
notoides, Idiosepius 1921a
nuculiformis, Crassinella 1940c
obstipa, Balcis (Vitreolina) 1954f
ochromphalus, Monadenia fidelis 1937b
Octopodoteuthidae 1912d
Octopoteuthidae 1912e
Oligochiton 1922c
oliveri, Polypus 1914b
Ommastrephoidea 1920a
opalescens, Loligo 1911c
Opeatostoma 1958d
oria, Polygyra columbiana 1933a
orina, Helminthoglypta 1938b
orotes, Epiphragmophora petricola 1920e
orotis, Vitrea 1930b
orthosymmetra, Turritella 1953c
ovuliformis, Pedicularia (californica?) 1946d
oxystoma, Micraenigma 1953c
pacifica, Placiphorella 1919a
pacifica, Rossia 1911c
pardus, Megalocranchia 1916d
parthenia, Pleuroliria 1957
patagiatus, Scaeurgus 1913c
pathopsis, Sandalops 1920h
Pegmapex 1960d
pella, Lepidozona 1963b
penicillifer, Octopus 1954c
pentedesmium, Cirsotrema 1963d
persephone, Opisthoteuthis 1918b
petricola, Epiphragmophora 1916a
petrothauma, Astraea (Pomaulax) 1940c
phoebe, Pegmapex 1960d
phorminx, Mitra (Subcancilla) 1969
phorminx, Mopalia 1919a
phyllura, Galiteuthis 1911c
pilsbryanum, Glyptosoma 1938c
pilsbryanus, Ischnochiton (Lepidozona) 1917h
pinicola, Polygyra 1916a
Ploiochiton 1926a
pluripuncta, Helminthoglypta tularensis 1938b
pluto, Opisthoteuthis 1918b
Polypodoidea 1920a
poormani, Conus 1968c
preposterum, Tiphyocerma 1958c
pricei, Polypus 1913b
princeps, Knefastia 1953c
pronotis, Monadenia fidelis 1931b
psaltes, Dendrochiton 1963b
punctocostata, Puncturella 1947d
punctulum, Mistostigma 1947d
puncturosa, Terebra (Strioterebrum) 1959d
pusilla, Diodora 1959d
pynca, Olivella 1935b
ralphi, Puncturella 1947d
regalis, Nematolampas 1913d
rehderi, Cantharus 1962
rhinetes, Nassarius (Schizopyga) 1953c
(Rhombochiton), Ischnochiton 1919b
ricaudae, Elaeocyma 1969
riparia, Helminthoglypta 1928a
rogersi, Lithophaga (Labis) attenuata 1957
rooseveltiana, Sonorella 1917e
rostae, Barbatia (Acar) 1954d
rotifer, Monadenia 1940b
rubescens, Octopus 1953e
rufa, Placiphorella 1917f
rufiterrae, Epiphragmophora tudiculata 1916a
saccharodytes, Helminthoglypta proles 1938b
sacculifer, Volsella 1953c
sanctaemonicae, Ischnochiton (Lepidozona) 1922c
sangabrielis, Epiphragmophora petricola 1920e
scarificata, Tivela 1940c
schencki, Actaeon (Microglyphis) 1941
scintillans, Abraliopsis 1911f
scolopes, Euprymna 1913c
scorpio, Polypus 1920h
scottiana, Monadenia fidelis 1940b
seftoni, Admete 1956b
semiliratus, Dendrochiton 1927b
semiusta, Mitra 1957
sentus, Acanthotrophon 1969
Sepioidea 1920a
shaskyi, Cantharus 1959d

shasta, Polygyra columbiana 1921e
sierrana, Polygyra 1921e
smithiana, Monadenia fidelis 1940b
sonorana, Bursa californica 1960d
sonorana, Stenoplax (Maugerella) conspicua 1956c
Sonorelix 1943
spectabilis, Tiariturris 1958c
spicata, Hanleya 1919c
spinicauda, Enoptroteuthis 1920h
Spiruloidea 1920a
stanfordiana, Acmaea 1957
Stearnsium 1958d
Stephanoteuthis 1909b
sticta, Pseudomelatoma 1956b
Stoloteuthinae 1914c
Stromboli 1954e
strongiana, Sonorella 1948a
subactum, Crucibulum 1963d
subtilis, Lepidozona 1956c
succinea, Lacuna 1953c
tejonis, Helminthoglypta 1938a
Tellidorella 1963d
tersa, Balcis (Balcis) 1954f
(Teuthidiscus), Opisthoteuthis 1918b
thamnopora, Mopalia (Dendrochiton) 1911e
thermimontis, Helminthoglypta 1953a
Tiariturris 1958c
Tiphyocerma 1958c
titubans, Balcis (Vitreolina) 1956b
torquifer, Turrigemma 1958c
trachypepla, Polygyra 1933a
Trialatella 1964a
tricoronis, Murex (Murex) 1960d
tridesmia, Clathurella (Glyphostoma) 1941
trigonura, Abralia 1913c
(Tripoplax), Ischnochiton 1919b
tuolumneana, Monadenia (Corynadenia) 1955b
Turrigemma 1958c
turrispira, Oenopota 1941
Turveria 1956d
tyrianthina, Acanthina 1957
tyrianthina, Neosimnia vidleri 1960d
ursipes, Spondylus 1959d
veligero, Octopus 1953e
Verrilliteuthis 1916d
Verticumbo 1940c
vortex, Oreohelix 1932b
walkeri, Knefastia 1958c
walkeri, Olivella (Macgintiella) 1958c
willetti, Antiplanes (Ractiplanes) 1953c
willetti, Epiphragmophora traskii 1920e
willetti, Ischnochiton (Lepidozona) 1917f
williamsi, Mactra (Mactra) 1960d
williamsi, Siphonaria 1969
williamsi, Woodbridgea 1953c
Woodbridgea 1953c
woodfordi, Mitromorpha barbarensis 1941
xenos, Vertigo allyniana 1919f
xerophila, Micrarionta 1922e
(Xiphiozona), Lepidopleurus 1919a
zizyphus, Clavus (Crassispira) 1940c

LIST OF NEW TAXA NAMED BY S. STILLMAN BERRY ARRANGED ALPHABETICALLY BY GENUS OR SUBGENUS. HIGHER TAXA ALSO INCLUDED IN ALPHABETICAL ORDER

Abralia astrolineata 1914b
Abralia astrosticta 1909b
Abralia trigonura 1913c
Abraliopsis scintillans 1911f
Acanthina tyrianthina 1957
Acanthotrophon sentus 1969
Acmaea acutapex 1960d
Acmaea concreta 1963d
Acmaea gabatella 1960d
Acmaea goodmani 1960d
Acmaea lepisma 1940c
Acmaea stanfordiana 1957
Acroteuthis 1913e
Acruroteuthis 1920g
Actaeon (Microglyphis) schencki 1941
Admete seftoni 1956d
Adontorhina 1947d
Adontorhina cyclia 1947d
Aequipecten (Leptopecten) camerella 1968c
Agaronia murrha 1953c
Amphitretoidea 1920a
Antiplanes (Ractiplanes) willetti 1953c
Antiplanes macfarlandi 1947d
Architeuthoidea 1920a
Argonautoidea 1920a
(Ascoteuthis) 1920h
Assiminea infima 1947b
Astraea (Pomaulax) petrothauma 1940c
Astraea guadalupeana 1957
(Austrorossia) 1918b
Balcis (Balcis) clavella 1954f
Balcis (Balcis) tersa 1954f
Balcis (Vitreolina) ebriconus 1954f
Balcis (Vitreolina) incallida 1954f
Balcis (Vitreolina) obstipa 1954f
Balcis (Vitreolina) titubans 1956b
Barbatia (Acar) rostae 1954d
Basiliochiton 1918c
Basiliochiton lobium 1925a
Benthoteuthidae 1912e
(Bessomia) 1959d
Botula cylista 1959d
Bursa californica sonorana 1960d
Calcitrapessa 1959c
Calliostoma grantianum 1940c
Callistochiton decoratus ferminicus 1922c
Callistochitoninae 1922c
Calliteuthis (Meleagroteuthis) heteropsis 1913b
Calliteuthis miranda 1918b
Cantharus rehderi 1962
Cantharus shaskyi 1959d
Cerithidea sacrata hyporhyssa 1906
Chaetopleura (Pallochiton) euryplax 1945a
(Chamaearionta) 1930a
Chiroteuthis famelica 1909b
Chiroteuthoidea 1920a
Chiroteuthoides 1920h
Chiroteuthoides hastula 1920h
Cirroteuthis macrope 1911c
Cirroteuthoidea 1920a
Cirostrema pentedesmium 1963d
Clathurella (Glyphostoma) tridesmia 1941
Clavus (Crassispira) zizyphus 1940c
Conus chrysocestus 1968c
Conus poormani 1968c
Coralliophila incompta 1960d
(Corynadenia) 1940a
Cranchia (Liocranchia) globula 1909b
Cranchioidea 1920a
Crania californica 1921b
Crassinella nuculiformis 1940c
Crenimargo 1963d
Crenimargo electilis 1963d
Crepidula coei 1950c
Crucibulum castellum 1963d
Crucibulum cyclopium 1969
Crucibulum monticulus 1969
Crucibulum subactum 1963d
Cyanoplax fackenthallae 1919a
Cymatioa 1964a
(Dendrochiton) 1911e
Dendrochiton laurae 1963b
Dendrochiton lirulatus 1963b
Dendrochiton psaltes 1963b
Dendrochiton semiliratus 1927b
Dimya californiana 1936
Dimya coralliotis 1944
Diodora pusilla 1959d
Diplodonta impolita 1953c
Diptychophilia 1964a
Discus (Gonyodiscus?) brunsoni 1955c
Elaeocyma baileyi 1969
Elaeocyma ricaudae 1969
Eledonella heathi 1911c
Enoploteuthis galaxias 1918b
Enoploteuthoidea 1920a
Enoptroteuthis 1920h
Enoptroteuthis spinicauda 1920h
Ensis myrae 1953b
Epiphragmophora petricola 1916a
Epiphragmophora petricola orotes 1920e
Epiphragmophora petricola sangabrielis 1920e
Epiphragmophora traskii chrysoderma 1920e
Epiphragmophora traskii willetti 1920e
Epiphragmophora tudiculata allyniana 1920e
Epiphragmophora tudiculata rufiterrae 1916a
Eucleoteuthis 1916d

Euprymna scolopes 1913c
Galeomma (Lepirodes?) mexicanum 1959d
Galiteuthis phyllura 1911c
Gemmula hindsiana 1958c
Glyptosoma pilsbryanum 1938c
Glyptosoma pilsbryanum binneyanum 1938c
Gonatus magister 1913b
Hanetia capitanea 1957
Hanetia macrospira 1957
Hanetia mendozana 1959d
Hanleya spicata 1919c
Helicocranchia fisheri 1909b
Helminthoglypta arrosa humboldtica 1938a
Helminthoglypta crotalina 1928a
Helminthoglypta dupetithouarsii consors 1938a
Helminthoglypta euomphalodes 1938b
Helminthoglypta graniticola 1926d
Helminthoglypta inglesi 1938b
Helminthoglypta isabella 1938b
Helminthoglypta jaegeri 1928a
Helminthoglypta liodoma 1938b
Helminthoglypta mohaveana 1926d
Helminthoglypta napea 1938b
Helminthoglypta orina 1938b
Helminthoglypta proles saccharodytes 1938b
Helminthoglypta riparia 1928a
Helminthoglypta tejonis 1938a
Helminthoglypta thermimontis 1953a
Helminthoglypta tudiculata angelena 1938a
Helminthoglypta tudiculata kernensis 1930c
Helminthoglypta tularensis pluripuncta 1938b
(Herpeteros) 1947c
Hertleinella 1958e
Hertleinella leucostephes 1958e
Hormospira 1958c
Idiosepius notoides 1921a
Ischnochiton (Lepidozona) amabilis 1917h
Ischnochiton (Lepidozona) asthenes 1919a
Ischnochiton (Lepidozona) californiensis 1931c
Ischnochiton (Lepidozona) gallina 1925b
Ischnochiton (Lepidozona) golischi 1919a
Ischnochiton (Lepidozona) interfossa 1917h
Ischnochiton (Lepidozona) nipponica 1918a
Ischnochiton (Lepidozona) pilsbryanus 1917h
Ischnochiton (Lepidozona) sanctaemonicae 1922c
Ischnochiton (Lepidozona) willetti 1917f
Joubiniteuthis 1920a
Knefastia princeps 1953c
Knefastia walkeri 1958c
Lacuna succinea 1953c
Laetmoteuthis 1913c
Laetmoteuthis lugubris 1913c
Lampadioteuthidae 1916d
Lampadioteuthis 1916d
Lampadioteuthis megaleia 1916d
Lapsigyrus 1958d
Lepidochitona keepiana 1948b
Lepidopleurus (Xiphiozona) heathi 1919a
Lepidozona inefficax 1963b
Lepidozona pella 1963b
Lepidozona subtilis 1956c
Leptochiton clarki 1922c
Leptochiton diomedeae 1917h
Lithophaga (Labis) attenuata rogersi 1957
Loliginoidea 1920a
Loligo etheridgei 1918b
Loligo opalescens 1911c
Loliolopsis 1929a
Loliolopsis chiroctes 1929a
(Lophochiton) 1925a
Lucapinella milleri 1959d
Lunaia 1964a
Lunaia lunaris 1964a
Lycoteuthidae 1914b
Mactra (Mactra) williamsi 1960d
Margarites (Lirularia) aresta 1941
Megalocranchia pardus 1916d
Melampus mousleyi 1964a
Melampus olivaceus californianus 1964a
Mesodon (megasoma, subsp.?) eritrichius 1939
Mesodon (megasoma, subsp.?) euthales 1939
Micraenigma 1953c
Micraenigma oxystoma 1953c
Micrarionta (Eremarionta) aetotis 1928b
Micrarionta (Eremarionta) avawatzica 1930f
Micrarionta (Eremarionta) borregoensis 1929b
Micrarionta (Eremarionta) callinepius 1930e
Micrarionta (Eremarionta) depressispira 1928b
Micrarionta (Eremarionta) inglesiana 1928c
Micrarionta (Eremarionta) melanopylon 1930f
Micrarionta (Eremarionta) micrometalleus 1930f
Micrarionta (Eremarionta) mille-palmarum 1930e
Micrarionta (Eremarionta) morongoana 1929b
Micrarionta aquae-albae 1922e
Micrarionta xerophila 1922e
Mistostigma 1947d
Mistostigma punctulum 1947d
Mitra (Subcancilla) phorminx 1969
Mitra (Tiara) calodinota 1960d
Mitra (Tiara) directa 1960d
Mitra (Tiara) lindsayi 1960d
Mitra montereyi 1920d
Mitra semiusta 1957
Mitromica 1958d
Mitromorpha barbarensis woodfordi 1941
Mitromorpha galeana 1941
(Mohavelix) 1943
Monadenia (Corynadenia) tuolumneana 1955b
Monadenia callipeplus 1940b
Monadenia chaceana 1940b

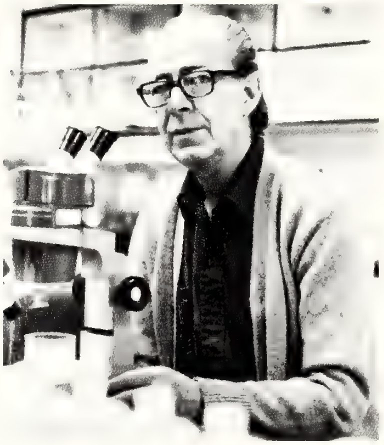
Monadenia cristulata 1940b
Monadenia fidelis callidina 1940b
Monadenia fidelis celeuthia 1927a
Monadenia fidelis klamathica 1937b
Monadenia fidelis leonina 1937b
Monadenia fidelis ochromphalus 1937b
Monadenia fidelis pronotis 1931b
Monadenia fidelis scottiana 1940b
Monadenia fidelis smithiana 1940b
Monadenia infumata alamedensis 1940b
Monadenia marmarotis 1940b
Monadenia rotifer 1940b
Moniliopsis chacei 1941
Mopalia (Dendrochiton) thamnopora 1911e
Mopalia chacei 1919a
Mopalia cirrata 1919a
Mopalia cithara 1951
Mopalia egretta 1919a
Mopalia phorminx 1919a
Moschites adelieana 1917a
Moschites albida 1917a
Moschites aurorae 1917a
Moschites challengeri 1916d
Moschites harrissoni 1917a
Murex (Murex) tricoronis 1960d
Murex carpenteri alba 1908a
Muricanthus callidinus 1958c
Nassa perpinquis bifasciata 1908c
Nassarius (Schizopyga) rhinetes 1953c
Nematolampas 1913d
Nematolampas regalis 1913d
Neosimnia bella-maris 1946b
Neosimnia catalinensis 1916e
Neosimnia vidleri tyrianthina 1960d
Nomaeopelta 1958d
Nomaeopelta myrae 1959d
Nucula (Ennucula) microsperma 1947d
Nuttalina crossota 1956c
Ocenebra crispatissima 1953c
Octopodoteuthidae 1912d
Octopoteuthidae 1912e
Octopus alecto 1953e
Octopous fitchi 1953e
Octopus hubbsorum 1953e
Octopus micropyrsus 1953e
Octopus penicillifer 1954c
Octopus rubescens 1953e
Octopus veligero 1953e
Oenopota turrispira 1941
Oligochiton 1922c
Oligochiton lioplax 1922c
Oliva ionopsis 1969
Olivella (Dactylidella) cymatilis 1963d
Olivella (Macgintiella) walkeri 1958c
Olivella (Olivella) fletcherae 1958c
Olivella pynca 1935b
Ommastrephes hawaiiensis 1912d
Ommastrephoidea 1920a
Opeatostoma 1958d
Opisthoteuthis californiana 1949a
Opisthoteuthis persephone 1918b
Opisthoteuthis pluto 1918b
Oreohelix californica 1931d
Oreohelix cooperi apiarium 1919g
Oreohelix flammulifer 1932b
Oreohelix handi jaegeri 1931d
Oreohelix nevadensis 1932b
Oreohelix strigosa canadica 1922b
Oreohelix vortex 1932b
Pecten (Leptopecten) euterpes 1957
Pecten lunaris 1963d
Pedicularia (californica?) ovuliformis 1946d
Pegmapex 1960d
Pegmapex phoebe 1960d
Pitar (Lamelliconcha) hesperius 1960d
Placiphorella pacifica 1919a
Placiphorella rufa 1917f
Pleuroliria artia 1957
Pleuroliria parthenia 1957
Ploiochiton 1926a
Polita gabrielina 1924a
Polygyra columbiana oria 1933a
Polygyra columbiana shasta 1921e
Polygyra hapla 1933a
Polygyra loricata nortensis 1933a
Polygyra pinicola 1916a
Polygyra sierrana 1921e
Polygyra trachypepla 1933a
Polypodoidea 1920a
Polypus (Pinnoctopus?) kermadecensis 1914b
Polypus apollyon 1912c
Polypus californicus 1911c
Polypus gilbertianus 1912c
Polypus hokkaidensis 1921c
Polypus hoylei 1909b
Polypus leioderma 1911c
Polypus madokai 1921c
Polypus oliveri 1914b
Polypus pricei 1913b
Polypus scorpio 1920h
Pseudomelampus mexicanus 1964a
Pseudomelatoma sticta 1956b
Pteropurpura (Centrifuga) deroyana 1968c
Pterygioteuthis microlampas 1913c
Ptychosyrinx chilensis 1968c
Puncturella punctocostata 1947d
Puncturella ralphi 1947d
Pyrgopsis lemur 1920h
Pyrgulopsis archimedis 1947a
(Rhombochiton) 1919b
Rimula californiana 1964a
Rimula mexicana 1969
Rossia (Aust[ro]rossia) australis 1918b
Rossia pacifica 1911c
Rossia pacifica diegensis 1912c
Sandalops ecthambus 1920h
Sandalops pathopsis 1920h
Scaeurgus patagiatus 1913c
Scissurella lyra 1947d
Sepia chirotrema 1918b
Sepia dannevigi 1918b
Sepia formosana 1912d
Sepia hedleyi 1918b
Sepiadarium austrinum 1921a
Sepiadarium nipponianum 1932a

Sepioidea 1920a
Siphonaria williamsi 1969
Skenea (?) cyclostoma 1941
Solenostiera gatesi 1963d
Sonorelix 1943
Sonorella anchana 1948a
Sonorella rooseveltiana 1917e
Sonorella strongiana 1948a
Spiruloidea 1920a
Spondylus ursipes 1959d
Stauroteuthis (?) mawsoni 1917a
Stearnsium 1958d
Stenoplax (Maugerella) conspicua sonorana 1956c
Stenoplax (Stenoradsia) heathiana 1946a
Stenoplax circumsenta 1956c
Stenoplax histrio 1945a
Stenoplax isoglypta 1956c
Stephanoteuthis 1909b
Stephanoteuthis hawaiiensis 1909b
Stoloteuthinae 1914c
Stoloteuthis iris 1909b
Stoloteuthis nipponensis 1911a
Stromboli 1954e
Teleoteuthis compacta 1913c
Tellidorella 1963d
Tellidorella cristulata 1963d
Terebra (Strioterebrum) danai 1958f
Terebra (Strioterebrum) fitchi 1958c
Terebra (Strioterebrum) puncturosa 1959d
(Teuthidiscus) 1918b
Teuthowenia (Ascoteuthis) corona 1920h
Thyca (Bessomia) callista 1959d
Tiariturris 1958c
Tiariturris spectabilis 1958c
Tiphyocerma 1958c
Tiphyocerma preposterum 1958c
Tivela scarificata 1940c
Transennella caryonautes 1963d
Trialatella 1964a
Trialatella cunninghamae 1964a
(Tripoplax) 1919b
Turcica admirabilis 1969
Turrigemma 1958c
Turrigemma torquifer 1958c
Turritella anactor 1957
Turritella orthosymmetra 1953c
Turveria 1956d
Turveria encopendema 1956d
Verrilliteuthis 1916d
Verticumbo 1940c
Verticumbo charybdis 1940c
Vertigo allyniana 1919f
Vertigo allyniana xenos 1919f
Vertigo modesta microphasma 1919f
Vitrea orotis 1930b
Volsella sacculifer 1953c
Woodbridgea 1953c
Woodbridgea williamsi 1953c
(Xiphiozona), Lepidopleurus 1919a

IN MEMORIAM

DR. CARL W. GUGLER

6 September 1920–16 February 1984



Friends, colleagues and students were saddened to hear of the death of Carl W. Gugler on February 16, 1984. He was a longtime member of the American Malacological Union.

Carl Gugler was born September 6, 1920 and grew up on a farm north of Woodbine, Kansas. After graduating from high school in 1938, he attended Kansas State University. His undergraduate work was interrupted in 1942 when he was drafted into the U.S. Army. He served as an instructor first in Springfield, Missouri and then at Camp Carson in Colorado Springs, Colorado, where he was stationed until 1946. At Camp Carson, Carl taught classes for trainees destined for medical field teams. He and another technician were also responsible for organizing a mosquito collection. The Army's malaria field teams would send various specimens of malaria carrying mosquitos to Camp Carson. The species were identified and preserved in a permanent collection. After his discharge, Carl and his wife Mary Anne (whom he married in 1945) returned to Kansas State University where he continued his studies, receiving his B.S. in 1948 and an M.S. in Zoology in 1949.

Carl began his teaching career in 1949 when he joined the faculty of Southwest Missouri State College as an instructor. Later he moved to Lindsborg, Kansas where he was an instructor at Bethany College from 1950–52. Carl came to the Department of Zoology of the University of Nebraska in Lincoln in 1952, serving as an instructor for eight years. During these years at UNL he worked toward his Doctor of Philosophy degree in Zoology. His dissertation research was a study of the myology of the least shrew *Cryptotis parva*. After receiving his Ph.D in 1959 Carl continued at UNL as an assistant professor in the Department of Zoology.

Some of us were fortunate enough to have been his students. Dr. Gugler was a teacher who inspired in us a special kind of interest and enthusiasm. He taught the subject of Invertebrate Zoology by comparing the functional systems as they existed throughout the phyla rather than by teaching one phylum at a time. The student was presented with the diversity of the invertebrate phlya in a manner which was clear and unified. In addition to the usual collection of preserved specimens, Dr. Gugler devoted a great deal of time to maintaining a large collection of live marine and freshwater animals available for students to observe and study. Professor Gugler's students were kept up-to-date with current research on invertebrates through access to an extensive reprint file which he maintained. In recognition of his teaching ability he received in 1969 the Distinguished Teaching Award in Science and Technology.

While at UNL, Dr. Gugler served as vice chairman (1967–71) and then as the last chairman of the Department of Zoology (1971–73) before the Department's merger into the School of Life Sciences. His activities at this time helped ease the transition for faculty and students alike.

Dr. Gugler's research interests were concerned with the reproduction and development of terrestrial gastropods. He travelled extensively throughout Nebraska, Iowa, Missouri, and Kansas on collecting trips. Several of the species he collected were maintained in a habitat which he constructed in his backyard, close to his personal basement laboratory. Carl's work was of the highest quality, but he

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chose not to follow the usual routine of publishing papers. He preferred instead to present his work directly to his fellow malacologists. The national meetings of A.M.U. were the primary means of disseminating his results. Many members of A.M.U. will be familiar with his work and know of the caliber of his research. Carl was an active member of A.M.U., involved in the reviewing of papers for the Bulletin. During these past two years he also served as Councillor-at-Large. He will be greatly missed.

Tom Bargar
Lincoln, Nebraska
21 March 1984

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SENTENTĬA

USE OF THE TERMS PROTANDRY, PROTOGYNY, AND HERMAPHRODITISM IN MALACOLOGY

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ABSTRACT

The terms protrandry, protogyny, and hermaphroditism have distinct and precise meanings to theoretical ecologists, reproductive biologists, and evolutionary biologists. However, some malacologists have used these terms in other ways, causing the theoretical workers to misunderstand and misapply the reproductive patterns of mollusks. "Protandry" should be used to describe animals that change sex from male to female without reverting to male at a later time. Likewise, protogyny involves a single sex change, from female to male, and is rare in the Mollusca. Only evidence obtained from the study of individual animals can be accepted as proof that sex change occurs. Age- or size-specific sex ratio data are circumstantial evidence requiring further substantiation.

> If investigators will keep facts clearly separated from interpretation and use principally either photographs or camera lucida drawings for illustration instead of diagrams, some future biological theorist may be able to unify all the numerous and diverse contributions to the study of sex and sex inheritance.
>
> (Grave, 1942)

Forty years after Grave made a plea for clarity in the primary literature on sexuality in mollusks, theoretical biologists are indeed trying to unify the patterns of sexuality, not only to understand mechanisms of sex inheritance, but also to explain both the evolution and ecological importance of life histories in terms of natural selection. Ghiselin (1969, 1974) was among the first to do so using mollusks. Hypotheses have been constructed to explain protogyny and simultaneous hermaphroditism with reference to fish (Warner et al., 1975; Leigh et al., 1976; Fischer, 1981). Protandry has been analyzed theoretically for mollusks (Hoagland, 1978) and for shrimp (Carpenter, 1978; Charnov, 1979). Authors of synthetic analyses without taxonomic emphasis such as Charnov (1982), Charnov et al. (1976), Heath (1977), and Clark (1978) rely on papers in taxon-oriented journals to provide their data bases. Such authors seek ecological similarities among species that possess a particular type of sexuality.

Unfortunately, the definitions of the sexual categories differ between some taxonomic-oriented authors and the theorists. The result is confusion in the analysis of patterns in invertebrate sexuality. Many theoretical ecologists accept at face value the terms used in the original literature without detailed inspection of the data upon which the definitions are based. Moreover, researchers sometimes have not proven unequivocally the type of sexuality a mollusk possesses.

The intention of this communication is to define the terms protandry, protogyny, and hermaphroditism as they are understood by zoologists working on the evolutionary ecology of sex and life history. I will show why these restricted definitions are useful and indeed necessary in analyzing patterns of sexuality. I will then give examples of inappropriate use of the terms, and will suggest the kinds of data malacologists should use in determining the patterns of sexuality of their taxa.

DEFINITIONS

Hermaphroditism in its broadest sense is the production of eggs and sperm by the same individual. Several categories are recognized that differ in terms of their functional morphologies as well as their effect on genetics (degree of outbreeding) and sexual structure. *Simultaneous hermaphroditism* is the simultaneous release of eggs and sperm by one organism using the same gonad to produce both eggs and sperm. Simultaneous cross-fertilization or self-fertilization can occur in some simultaneous hermaphrodites (e.g., some land snails). However, more often, the eggs and sperm do not become mature and capable of fertilization exactly at the same time. In land snails, the male function usually occurs first. Kraemer (1983) reported that in the freshwater clam *Corbicula*, eggs begin to ripen first, followed by sperm development; the products become fully mature simultaneously and self-fertilization is thought to be a possibility. In some other bivalves, sperm development begins prior to egg development, but there is much intraspecific variation in the timing of the development of sex products in bivalves. While Clark (1978) suggested in the term *opsiautogamy* for sequential egg and sperm ripening culminating in self-fertilization, I agree with Policansky (1982) that this term in unncessary. Policansky himself erected *sequential cosexual* to describe animals that have sequential egg and sperm ripening in the same season, whether self-fertilizing or not. I believe the main focus should be on the fact that such animals are still simultaneous hermaphrodites using the same organ to produce eggs and sperm within the same season. If we limit simultaneous hermaphroditism to those species that produce mature eggs and sperm exactly at the same time, we will have defined the term almost out of existence.

Animals that function first as one sex, then as another, repeatedly, possess *alternating sexuality*. Coe (1934a) used this term to describe certain bivalves. He reported that *Crassostrea virginica, Ostrea lurida*, and *O. gigas* alternate sex, while the gonad remains basically bisexual. In some species however, the first gonad may break down and cells differentiate as a new gonad of the opposite sex. Sometimes the individual functions as one sex for a whole season; other times it spawns as one sex and then the other in the same summer (reported for *Teredo navalis* by Coe, 1943). Usually the male gametes develop first (Coe, 1934b; 1936). Coe started confusion in the molluscan literature by calling animals that begin their life of alternating sexuality as males "protandric, with a rhythmical series of alternating sexual phases" (Coe, 1934a). However, protandry and alternating sexuality are mutually exclusive.

An ecological explanation of alternating sexuality is that sperm can be produced with less energy and developmental time than eggs, and are produced when the organism is energy-limited or short of certain particular nutrients required for egg production (Kennedy, 1983). However, this hypothesis has not been rigorously tested, and is not an attractive explanation for cases in which sex change occurs out of phase with nutrient availability. The sex ratio of populations with alternating sexuality is extremely labile. Herlin-Houtteville and Lubet (1975) reviewed the sexuality of bivalves, and emphasized that within a single genus, species that are simultaneous hermaphrodites and those with alternating sexuality have been reported. There may also be substantial error in the assignment of bivalves to sexual categories. But there is nonetheless a blurring of the distinction between simultaneous hermaphroditism and alternating sexuality. It becomes a matter of degree of separation of the ripening and release of male and female sex products.

Charnov (1979) and Policansky (1982) consider hermaphroditism to be simultaneous if male and female gametes are both produced in the same breeding season. While this definition separates the two terms, the separation does not reflect biological reality. In the Teredinidae and the oysters, animals often breed as males soon after breeding as females . . . . . is this the same breeding season? What of warm-water species that have no discrete breeding seasons but nevertheless alternate sexuality? *Crepidula* species change sex only once, but often do so within a breeding season; no one would call them simultaneous hermaphrodites for that one season. One alternative is to consider alternating sexuality to occur when the gap between male and female function is large enough that neither simultaneous cross-fertilization nor self-fertilization can occur. A further complication is that storage of viable sperm could lead some mollusks to self-fertilize even when they appear to have temporally-separate sexual functions. Detailed study of many marine hermaphrodites may show them actually to have alternating sexuality.

Sequential hermaphroditism is a general term for the temporally-separated function of an organism first as one sex, then as the other. Most authors restrict the term to protandry and protogyny (Charnov, 1979). Obviously, the term is not specific enough to be used without further information. So too with *sex change* and *sex reversal*, which are used synonymously and could refer to protandry, protogyny, or even alternating sexuality.

Protandry is the functioning of an organism first as male, then as female, with no further sex change. The two sexual phases are separated by a phase in which male primary and secondary sex characters disappear, and the animal re-differentiates as a female. In *Crepidula* for example, the penis is resorbed or reduced in size. There is some question as to whether, in most protandrous species, the gonad re-differentiates or whether the female gonad is an entirely separate structure. Protandry is most uniformly found in the marine gastropod family Calyptraeidae, though it is reported in many other molluscan families. *Protogyny* is the opposite of protandry; the organism first differentiates as a female, then re-differentiates as a male with no further change.

Protogyny has been attributed to mollusks rarely, and is not expected on theoretical grounds (Hoagland, 1978; Charnov, 1982). The basic ecological-evolutionary theory is that sex change from male to female is advantageous when a species can reproduce more with increase of size as a female, but size (or age) increase is not important to male fecundity. This is true of many mollusks in which brood size and fecundity are proportional to female size, but the ability for a male to successfully fertilize females may be even enhanced by small size (Hoagland, 1978). On the other hand, protogyny is common in fish in which the male defends a nest or a territory, and large size is important in his acquiring mates (Leigh et al., 1976; Charnov et al., 1976). In both protandry and protogyny, environmental factors often control the timing of sex change, and the sex ratio of a population can be related to its density or age structure (Hoagland, 1978; Charnov, 1979).

APPLICATIONS

From the preceding definitions, it is clear that there are functional and structural differences between one-time sex change, alternating sexuality, and simultaneous hermaphroditism. These differences affect the sex ratio, effective population size, and the degree of inbreeding of a population. If these three terms are defined as above, one can distinguish species that potentially self-fertilize from those that cannot; those with future labile sexuality from those that are fixed in sex once mature; those that change sex based on environmental factors from those whose hermaphroditism is continuous. Table 1 summarizes some ecological, genetic, and morphological differences between these three major types of sexuality.

The only certain way to distinguish among the types of hermaphroditism and sex change is to follow the lives of single individuals (Wright and Lindberg, 1979). Collecting mature sex products, observing functional change of external sex characters, or observing brooding provides conclusive evidence on functional sex change. Histological sectioning is sometimes ambiguous and more importantly it destroys the animal so that the temporal element unequivocally establishing the type of hermaphroditism is lost. Grave (1942), in sectioning the gonads of brooding females, was able to find maturing sperm. This is the best situation in which sectioning an individual can serve as positive evidence for sex change. Attribution of sex change is often based on circumstantial evidence, such as age and size. However, the presence of small males and large females is insufficient evidence for protandry (Wright and Lindberg, 1982). Subramoniam (1981) dissected numerous individuals of a mole crab and observed total sexual re-differentiation, which was conclusive as to sex change, but could not totally rule out alternating sexuality as opposed to protandry.

The greatest confusion on sexuality seems to be in the literature on marine bivalves, including oysters and Pholadacea. Workers have reported protandry, protogyny, alternating sexuality, and gonochorism all in the same species (Choquet, 1970, summary table p. 401). The genera *Bankia* and *Teredo* and some *Ostrea* species have been assumed to be protandrous. However, a re-examination of the literature (Coe, 1933, 1934a and b, 1936, 1941, 1943; Orton, 1927, 1933; Grave, 1942) shows that alternating sexuality (either in different breeding seasons or within the same season) is more accurate for most of these species studied so far. Asif (1979) correctly cautioned that size-sex data in tropical *Crassostrea* only suggest sex change; dwarf males and delayed female maturity could produce a pattern mimicking protandry. Yet Policansky (1982) quoted his work as demonstrating protandry. In general, the attribution of sexual types to mollusks quoted by Policansky should not be taken at face value, but should be checked against the original data and any recent work for confirmation, based on the definitions of sexual types and whether or not the data are sufficient to prove the case. One must also be careful not to attribute a mode of sexuality to all members of a genus or a family when only a few have been studied.

The freshwater bivalves are not without confusion as well. Evidence for some form of sequential hermaphroditism in species of *Corbicula* is circumstantial; at different times *C. fluminea* has been called both protandrous and protogynous (e.g., Morton, 1982, 1983). Nor have marine gastropods escaped the problem: Robertson (1981) used only size-sex data to state that *Epitonium albidum* is protandrous "with only one sex change." However, the greatest confusion in the use of "protandry" comes from entomologists, several of whom use the term for the case where males hatch before females (Fagerstrom and Wikland, 1982).

Table 1. Functional and structural differences between simultaneous hermaphroditism, one-time sex change, and alternating sexuality.

Character	Simultaneous Hermaphroditism	Protandry, Protogyny	Alternating Sexuality
Sex Ratio	Meaningless	Often density- or age-dependent	Often dependent on environmental conditions (food)
Self-fertilization	Possible	Rarely possible	Rarely possible
Labile sexuality	No	Not once mature	Yes
Effective population size vs. total population size	1:1	< 1	< 1
Gonad	Bisexual	Male or Female. New differentiation of gonadal material at sex change.	Bisexual; or newly differentiated at sex change.
Secondary sex characters	Usually lacking	Often well-developed animal externally recognizable as ♂, ♀, or re-differentiating (esp. in fish)	Usually lacking

Malacologists and other invertebrate zoologists should avoid calling an organism protandrous or protogynous unless the necessary evidence obtained from sufficient individuals is also reported. It will greatly aid research on sexuality if the major categories "simultaneous hermaphroditism", "protandry", "protogyny", and "alternating sexuality" are used in the same manner by researchers in different but inter-dependent disciplines.

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RESEARCH NOTE

A SIMPLE TECHNIQUE FOR REARING *BIOMPHALARIA GLABRATA* IN THE LABORATORY

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The culturing of *Biomphalaria glabrata* (Say, 1818) in the laboratory presents problems that have been solved by several methods (Chernin and Michelson, 1957a, b, *American Journal of Hygiene* 65: 57–70 and 71–80; Chernin and Schork, 1959, *American Journal of Hygiene* 69: 146–150; Vieira, 1967, *American Journal of Tropical Medicine and Hygiene* 16: 792–796; Senna and Vieira, 1970, *American Journal of Tropical Medicine and Hygiene* 19: 568–570; Sturrock and Sturrock, 1970, *Annals of Tropical Medicine and Parasitology* 64: 349–355; Thomas, 1973, *Journal of Zoology London* 172: 443–467; De Souza et al., 1977, *American Journal of Tropical Medicine and Hygiene* 26: 1013–1017). In most instances, even the best systems seem to require an inordinate amount of time to prepare special foods, make daily changes from degraded lettuce to fresh leaves, clean pans, and maintain complex lighting and aeration systems. The following describes a system requiring no special food and once a year maintenance.

Water from a freshwater lake was collected (one time only) and sterilized by boiling (even dechlorinated city water is often toxic). Whenever water levels need to be replenished, deionized water is added to the tanks. When the tanks are cleaned (once a year), the "old" water is saved, added back to the clean tank, and brought up to the necessary volume with deionized water.

The tanks hold 10 gallons of water and are equipped with standard undergravel filters overlaid with a 2″ layer of white aquaria rocks. One Gooseneck lamp with a 60 watt bulb is placed next to the tank (where the bulb is within 1″ of the glass) and used for both light and heat. These lamps are on 24 hours a day.

The snails feed, in part, on the algae that has established colonies in the tanks (algal samples are retained when the tanks are washed). However, every two weeks or whenever there is a need to increase the snail population, 1 or 2 tablespoons of Purina rabbit chow 5321 (complete formula) are added to the tanks (these pellets do not foul the water). Whenever axenic conditions are desired, the pellets can be autoclaved for 15 minutes at 15 lbs. pressure at 110°C without affecting results. The culture techniques described have been successfully utilized for 13 years.

Since food is often the critical component in a culture situation, experiments were performed to compare the relative longevity, growth rates and egg producing capabilities of snails maintained in individual containers and fed romaine lettuce *or* rabbit chow. Conditioned aquarium water was used. Each dish was cleaned and the water was changed daily. All experimental animals were 2–3 weeks old and 2–3 mm in diameter at the start of each trial. Prior to being transferred, the F_0 animals had been raised in an environment containing both chow and algae. Subsequent generations were obtained via self-fertilized snails and exposed *only* to the diets specified in each experimental situation. Lettuce-fed animals (7 trials) maintained in 200 ml of water lived an average of 48.9 days and laid approximately one egg mass every other day. Lettuce-fed animals (12 trials) maintained in 750 ml of water survived an average of 58.9 days and laid approximately 1 egg mass each day. All subsequent trials were performed in 200 ml of water because those conditions were the least conducive to normal survival (12 months +) and fecundity; therefore, changes in diet should have the greatest impact.

When F_1 offspring of the above snails (self-fertilized) were cultured on lettuce (24 trials) the survival times mimicked the above results; however, no eggs were laid. F_2 offspring (24 trials) fed lettuce, again survived an average of 50 days and laid no eggs (snails normally produce eggs by the sixth week; these animals were nine weeks +). All of the above snails had an average shell size of 5 mm at the time of death. One surviving F_2 was fed rabbit chow on the 50th day and eggs were produced within 5 days. The resulting F_3 offspring were separated into 2 groups, lettuce-fed (18 trials) or rabbit-chow-fed (18 trials). Lettuce-fed F_3 snails all died within a 39–63 day span, produced no eggs and averaged 5 mm shell size. Rabbit-chow-fed F_3 snails *all* survived the length of the experiment (65 days), laid eggs daily, and averaged 12 mm shell size when terminated. Daily growth rates for lettuce-fed and rabbit-chow-fed snails were also compared (0.094 mm/day and 0.153 mm/day respectively). An one way ANOVA showed that all differences between lettuce-fed and rabbit-chow-fed snails were significant ($p < .01$). These data support the contention that compared to romaine lettuce, rabbit chow is a superior food supply for *Biomphalaria glabrata*. it would be interesting to determine the effects of a rabbit-chow-diet on other species of fresh water and land snails.

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THE AMERICAN MALACOLOGICAL UNION
50th ANNUAL MEETING

NORFOLK, VIRGINIA, U.S.A.
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ABSTRACTS
POSTER SESSION

PHYSICAL ALTERATION OF THE STRUCTURE OF THE HARD-SHELLED CLAM, *MERCENARIA*. **Elana Benamy,** Academy of Natural Sciences of Philadelphia, Pennsylvania.

A sequence of shells of the genus *Mercenaria,* ranging in age from modern to Miocene, was examined using the scanning electron microscope (SEM). The objectives of this study were to document and describe the progressive degradation of the crystalline structure of the shell and to evaluate this examination process as an indicator of shell preservation.

The shells examined contain four different shell structures. Of these, the composite prismatic structure, because of the predictability of its occurrence and the smooth surfaces, sharp angles, and regular arrangement of its structural units, was found to be the most reliable indicator of shell alteration.

Based on the microscopic examination, the shells were divisible into three groups, unaltered, slightly altered and strongly altered. There was good correlation between the age of the fossils and the condition of shell microstructures. Furthermore, the nature of the visible changes, and absence of depositional features or any detectable alteration of the original aragonite to calcite, suggests that the diagenetic processes the shells had been exposed to were mainly dissolutional.

Finally, several slices of modern shell were pyrolyzed in water and nitrogen to see if the induced alteration of the shell structure would mimic natural diagenesis. Because of the radically different appearance of the pyrolyzed shells as well as the variability in the intensity of alteration (even within the same slice) pyrolysis is probably not a valid technique to use to simulate diagenesis of shell microstructures.

CONTRIBUTIONS TO THE FIELD ECOLOGY OF *DONAX FOSSOR* (SAY 1822) ROCKAWAY BEACH, LONG ISLAND. **Bernard J. Blum,** Rockaway, New York.

Collections of *Donax fossor* (Say 1822) were made for over a decade to suggest it is a regular infaunal component of Rockaway's sandy beaches. Dredging of juveniles in the months of April, October and June, and beach collections of juveniles from late May to early July suggest a subtidal setting of hardy juveniles that overwinter to colonize beaches the following year. Gonadal analysis, winter collections of several adults, marking experiments, and shell collections provide supporting evidence for a life cycle.

Density studies show that all beach populations, from just inside East Rockaway Inlet to Breezy Point, are migratory. The position of the density peak at low tide is a function of population mean, wave energy, length of the intertidal zone, air temperature and water temperature. Comparison of all peaks suggest that populations are following the ebb tide line for feeding purposes.

On the flood, observations suggest that an internal rhythm accounts for leaping and burrowing movements. On the ebb, clams do leap into the backwash, but several observations suggest that an internal rhythm may also be involved in this movement. Acoustic shock, moisture and thixotropic changes in the sand are discounted as releasing stimuli to flood and ebb tide behavior. Backwash that leaves migrating clams emergent does stimulate burrowing.

A PRELIMINARY COMPARISON OF REPRODUCTIVE PHENOLOGIES IN A FRESHWATER MUSSEL COMMUNITY. **Walter R. Hoeh,** Museum of Zoology, University of Michigan, Ann Arbor, and **Richard J. Trdan,** Department of Biology, Saginaw Valley State College, University Center, Michigan.

In April of 1982, an investigation was initiated to determine the timing of fertilization, the duration of larval development, and the period of glochidial release for a lotic freshwater mussel community. The study site, a 150m reach of the Cedar River immediately down stream from Chappel Dam, is located in Gladwin County, Michigan. Mean stream width is 30m with depth ranging from 0.2–1.5m. Summertime current velocity in this low gradient, hardwater stream is less than 0.5m/sec. The freshwater mussels present at the site, in decreasing order of abundance, include *Anodonta grandis, Actinonaias ellipsiformis, Lampsilis radiata, Anodonta imbecilis, Lampsilis ovata, Lasmigona compressa, Fusconaia flava,* and *Anodontoides ferussacianus.*

A total of 42 observations (minimum of 1/month) were made on the mussel community between April 1982 and June 1984. Assessment of mussel gravity, state of larval development (which was used to infer approximate fertilization time), and glochidial release period were based on external marsupial morphology and microscopical examination of marsupial contents from hand-picked specimens. In addition, water temperature and relative depth were recorded for each sampling date.

Fertilization in *A. grandis, A. ellipsiformis, L. radiata, L. ovata, L. compressa,* and *A. ferussacianus* occurred in July–August. This coincided with maximal water temperature (~25°c) and minimum water depth. In *F. flava,* fertilization occurred in early June 1983 and in early May 1984 with water temperature ranging from 14–15°C. Fertilization in *A. imbecilis* occurred from May through August, beginning when the water temperature approached 14°C. Larval maturation for *A. grandis, A. ellipsiformis, L. radiata, L. ovata,* and *L. compressa* was completed within 7–8 weeks.

A. grandis initiated glochidial release in mid-February with water temperature ranging from 1–3°C. This was followed by (1) *A. ferussacianus* (early April, 5°C), (2) *L. compressa* and *A. ellipsiformis* (mid-April, 10°C), and (3) *L. ovata* and *L. radiata* (late-April, 14–15°C). The length of the glochidial release period was 12 weeks for *A. grandis* and *A. ellipsiformis,* 10 weeks for *L. radiata* and *L. ovata,* and 7 weeks for *L. compressa.* In *A. imbecilis* glochidial release began in March (4–5°C) and ended in October. The extended duration of the release period is probably due to the extended fertilization period noted above.

CONCHOLOGICAL SPECIES PAIRS OF WESTERN ATLANTIC 'ACTEOCINIDS'. Paula M. and Paul S. Mikkelsen,

Harbor Branch Foundation, Inc., Ft. Pierce, Florida.

Three species pairs of Western Atlantic *Acteocina/Tornatina* (Gastropoda: Cephalaspidea) are defined. Each pair consists of two conchologically similar morphs which differ primarily in protoconch type, indicating different types of larval development: direct (relatively unknown among cephalaspids) or planktonic. Radular and gizzard plate morphological data, taxonomically important in this group at the generic level, are incomplete for 2 of the 3 pairs.

Members of Pair #1, consisting of *Acteocina candei* (Orbigny, 1841) and an unnamed *Acteocina* sp., exhibit smooth, thick-walled, spindle-shaped shells, with extended spires, ribbed subsutural sculptural bands, and single-plaited columellas of typical form for the group. Members of Pair #2, consisting of "*Tornatina*" *liratispira* E. A. Smith, 1872, and *Acteocina lepta* Woodring, 1928, exhibit spirally-striate, thick-walled, columnar shells, with low spires, ribbed and double-keeled subsutural bands, and typical columellas. Members of Pair #3, consisting of *Tornatina inconspicua* Olsson and McGinty, 1958, and "*Tornatina*" *decurrens* Verrill and Bush, 1900, exhibit smooth, thin-walled, columnar shells, with low spires, narow concave subsutural bands, and thickened columellas. [Quotation marks surrounding genera reflect the uncertain placement of species with unknown radula and gizzard plate morphologies.]

Although geographic distributions overlap for each pair, limited evidence derived from museum material shows that pair-members are rarely sympatric. Reproductive anatomy has been only partially described for both members of Pair #1, with inconclusive results, and is entirely unknown for all others. The existence of these species pairs may indicate (a) convergent evolution of conchological features (= 2 species per pair), or (b) poecilogony (multiple types of larval development in a single species) (= 1 species per pair).

CARETTA CARETTA AS HABITAT: MOLLUSCS AS EPIFAUNA ON THE LOGGERHEAD SEA TURTLE. Kathryn A. Muldoon,

Applied Biology, Inc., Jensen Beach, Florida.

Macroinvertebrate epifauna collected from 48 Loggerhead sea turtles on the east coast of Florida were analyzed and found to contain three different types of molluscs; sessile, or fouling species; boring bivalves; and motile predatory gastropods. The first two were generally associated with barnacles, while motile gastropods were usually found to inhabit the fleshy pocket between the turtle's tail and carapace. Species names, numbers of individuals and taxa, and individual sizes of all molluscs were recorded and compared with the length, weight, condition, and sex (when determined) of the host turtle. Thirty-nine percent of the Loggerheads sampled from March, 1983–April, 1984 contained molluscs. The possible biogeographic implications of the turtle-mollusc relationships has been examined. The connection between the presence of motile gastropods in the turtle's "pocket" and the incidence of spirorchidiasis (blood flukes) in sea turtles has also been examined.

MOLLUSCAN RATES OF COLONIZATION OF SEDIMENT AT FOUR DEPTHS OFFSHORE OF CENTRAL EASTERN FLORIDA. Robert W, Virnstein and Paul S. Mikkelsen,

Harbor Branch Foundation, Inc. Fort Pierce, Florida.

Rates of colonization of defaunated sediments were estimated by comparing densities and diversities of molluscs in sediment boxes with those in natural sediments at 33 m, 124 m, 187 m, and 311 m offshore of Ft. Pierce, on the central, eastern coast of Florida. A total of 22,137 molluscan specimens were collected, representing 280 species. Bivalves were most numerous (15,945), followed by gastropods (4,241), scaphopods (1,618) and aplacophorans (333). Gastropods were most speciose (134 spp), followed by bivalves (108 spp.), aplacophorans (22 spp.) and scaphopods (16 spp.). Natural densities were highest at 33 m, and decreased to 124 m, to 311 m, with a minimum at 187 m, while diversities were highest at 33 m, and decreased to 311 m, to 124 m, and to 187 m.

Considering the Mollusca as a whole, diversity of Mollusca in initially defaunated sediment boxes exceeded or equalled natural diversity by experiment termination (particularly at the two shallower sites) except at the 311-m site where molluscan diversity had only attained 80% natural diversity. The time to attaining natural diversities increased with increasing depth. Densities of gastropods and bivalves in sediment boxes were highest at 33 m. Bivalve diversity in the experimental samples exceeded natural diversity at all sites except the 311-m site. Scaphopod diversity was generally low in sediment boxes, with a minimum at 187 m and a maximum at 124 m. Highest colonized diversity of aplacophorans was at 311 m, followed by 187 m, and 124 m; they were absent at 33 m.

Colonization rates, of Mollusca as a whole, decreased from sites at 33 m, to 187 m, to 124 m, to 311 m. For total Mollusca, experimental samples attainined natural densities in about 3 wk at 33 m, 5 wk at 187 m, and 35 wk at 124 m, and only 60% natural density after 64 wk at 311 m. Densities in experimental boxes exceeded natural densities at all sites except at 311 m. The 33-m experimental population began to decline sharply within 6 wk; at all sites except 311 m the experimental densities had not decreased below natural levels by the termination of the experiments: 21 wk at 33 m, 45 wk at 124 m, 51 wk at 187 m, and 64 wk at 311 m.

Gastropods were the fastest colonizers at all depths, surpassing natural densities within a few weeks, although fastest at 33 m (1 wk), followed by 187 m (2 wk) and 124 m (3 wk), and were slowest at 311 m (7 wk). Bivalves colonized least rapidly at 311 m, not reaching natural densities after 64 wk, but exceeded natural densities at other sites within the experimental time period. Scaphopods colonized fastest at 311 m, and attained only ⅔ natural densities in 45 wk at 124 m, where they were most abundant in natural sediments. Aplacophorans showed the least ability to colonize, attaining about ⅓ natural densities by 51 wk and 64 wk at the 187-m and 311-m sites, respectively. Highest molluscan density, diversity, and colonization rates occurred at 33 m, with a general decline in all three parameters with increasing depth.

LOW TEMPERATURE TOLERANCE OF WINTER-ACCLIMATED *CORBICULA FLUMINEA*. Patricia A. White and **Albert J. Burky,** University of Dayton, Ohio.

The northern distribution of the Asiatic clam, *Corbicula fluminea* (Müller), has been claimed to be associated with thermally buffered waters. This theory has been supported by published data on distribution, and by studies of low thermal tolerance where clams (laboratory acclimated) do not survive below 2° C.

In this study, winter field-acclimated juveniles and adults (Great Miami River, Dayton, OH) were examined for survival at experimental temperatures of 0, 2, 5, and 15°C. A field acclimation temperature of 0°C was determined as the average field temperature two weeks prior to collection. Clams were collected and held at 0°C for eight days prior to tolerance testing. Groups of 20 juveniles (1–10 mm, shell length) and 14 adults (10–40 mm) were fed daily during testing at each experimental temperature for 1266 h (52.8 d). Observations for mortality (M) were made at 6 h intervals for the first month, and every 24 h thereafter. M was determined by a 'gape' and 'twist' test. For each experimental group the relationship of time (T) in hours *vs* % M can be expressed by $M = a + b \ln T$, where 'a' and 'b' are constants. At 0°C the first Ms were at 411 h (17.1 d) and 892 h (37.2 d) with 50% Ms at 683 (28.5 d) and 1266 (52.8 d) for juveniles ($a = -501.12$, $b = 84.51$, $r^2 = 0.97$) and adults ($a = -544.72$, $b = 80.56$, $r^2 = 0.61$) respectively. Fifty % M was not reached at other test temperatures. At 2°C the first Ms were at 621 h (25.9 h) and 892 (37.2 d) for juveniles ($a = -409.56$, $b = 64.16$, $r^2 = 0.92$) and adults ($a = -426.12$, $b = 63.48$, $r^2 = 0.82$) respectively. At 5°C the first Ms were at 531 h (22.1 d) and 823 h (34.3 d) for juveniles ($a = -354.74$, $b = 56.38$, $r^2 = 0.94$) and adults ($a = -480.87$, $b = 72.15$, $r^2 = 0.90$) respectively. No M was observed at 15°C. These data show that *C. fluminea* can tolerate prolonged exposure ($>$ 53 d) at temperatures below 2°C, and that adults are more tolerant than juveniles. The northern distribution of *C. fluminea* may be limited more by summer constraints on reproduction (due to "low" temperature regimes) than by winter survival.

***ELLIPTIO LANCEOLATA:* WAS ISAAC LEA'S ORIGINAL DESCRIPTION PROPER AFTER ALL? Douglas A. Wolfe,** National Oceanic and Atmospheric Administration, Rockville, Maryland.

Elliptio lanceolata (Lea, 1828) was originally described from the Tar River in North Carolina, based on a form with a smooth, shiny, yellowish elongate shell (illustrated by Johnson, 1970 in fig. 2, Plate 11). Johnson (1970: Bull. Mus. Comp. Zool. 140:263–449) synonymized numerous elongate species of *Elliptio*, most of them described by Lea, under the name *E. lanceolata*, including *E. angustatus* Lea 1831, *E. productus* Conrad 1836, *E. fisherianus* Lea 1838, *E. foliculatus* Lea 1838, *E. emmonsii* Lea 1857, *E. hazelhurstianus* Lea 1858, and *E. subcylindraceus* Lea 1873. The synonymy was based exclusively on conchological characteristics, and included essentially all the lanceolate *Elliptio* forms from the Atlantic coastal drainages, with a length/height ratio greater than two, except for *E. shephardiana* (Lea) from the Altamaha River.

Lea's original phenotype for *E. lanceolata* is readily distinguished from other forms (see Plates 10 and 11 in Johnson, 1970). The shell is shiny, yellowish and without rays. It has a smoothly rounded posterior ridge and pearly white nacre. The other forms have dark periostracum and/or greenish rays, a notable posterior ridge, and irridescent bluish nacre. Examination of the lots in the U.S. National Museum indicated that the *E. lanceolata* phenotype is sympatric with the *E. productus* (*or E. fisherianus*) phenotypes in the following river systems: Patuxent, Potomac, Rappahannock, James, Tar and Neuse. The *E. productus* and/or *E. fisherianus* phenotypes occur in addition in the Delaware, Susquehanna and Maryland Eastern Shore drainages to the north, and in at least the Cape Fear and St. Johns drainages to the south. Numerous other phenotypes occur also in rivers between North Carolina and Florida.

Davis et al. (1981: Biol. J. Linn. Soc. 15:131–150) examined three phenotypes of the *E. lanceolata* group for genetic similarities based on electrophoretic patterns for a suite of enzymes. The three phenotypes were: *E. fisheriana* from the Nanticoke River in Delaware, *E. foliculata* (Lake Waccamaw, N.C.), and *E. producta* (labeled as *E. lanceolata* by Davis et al.), also from Lake Waccamaw. This study revealed that genetic dissimilarity among the three phenotypes was sufficient to warrant full species status for all three. According to Davis et al: "the only cohesion among (these) species of the *E. lanceolata* group that justifies recognizing it as a distinct entity is the lanceolate shape." They considered the lanceolate shape therefore to have undergone parallel evolution in this genus.

Based on the genetic distinction between the sympatric Waccamaw phenotypes and between the similar *E. fisheriana* and *E. producta* phenotypes, I hypothesize that the original *E. lanceolata* Lea phenotype should once again be separated from *E. producta* and *E. fisheriana*. The very distinctive conchological characters of *E. lanceolata*, and its sympatric associations with *E. producta* and *E. fisheriana* only in the central portion of their range, lend further credibility to this hypothesis. A major reexamination of the relations among these, and possibly certain other forms clustered by Johnson under *E. lanceolata*, seems warranted.

ABSTRACTS
INVITED PAPERS
"MALACOLOGICAL MEDLEY"

SIZE, SHAPE AND STRUCTURE OF SNAIL SHELLS. Alan J. Kohn, Department of Zoology, University of Washington, Seattle.

Biomineralization processes, roles of organic matrix, and diversity of crystal architecture in relation to strength and other mechanical properties are currently active areas of study that suggest many opportunities for significant future research on snail shells. Because of their importance to the gastropods, I emphasize the following aspects:

1) *Geometry of shell growth.* In 2-dimensional section, snail shell growth fits the equiangular spiral formalized by Descartes in 1638 and applied to gastropods 200 years later by Moseley. Significantly, it is the only spiral that retains the same shape as it increases in size. Models of 3-dimensional shell growth based on this spiral provide objective, quantitative descriptors for taxonomy, aid understanding of the relationships of shell structure and function, and allow evaluation of the effects on shell shape of manipulating one or more parameters of shell growth separately or together.

2) *Crystal architecture.* Snails employ several types of $CaCO_3$ crystal architecture; most of these are analogous to construction materials employed by humans. For example, cross-lamellar structure, characteristic of neogastropod shells, is an analogue of plywood. Primary lamels branch and interdigitate, and their adjacent secondary lamels are oriented at about 80° angles to each other. In adjacent shell layers, the long axes of primary lamels are approximately at right angles. These interwoven orientations make the entire shell fabric stronger than alternative arrangements.

3) *Dynamics of shell growth: interior remodeling.* Some neogastropods, of which *Conus* is the best example, maintain a uniformly thick last whorl as a defense against crushing predators, but they dissolve most of the inner walls, reducing shell weight and increasing living space without sacrificing the first line of defense. In addition, $CaCO_3$ is added from within to weak parts of the shell, the spire and anterior tip of the columella.

4) *External shell sculpture.* Asymmetric sculptural elements in the form of ridges and tubercles have been shown to function as ratchets, facilitating burrowing by large, turritelliform gastropods in coarse sediments. Several independent lines of evidence suggest that asymmetric tubercles and ridges similarly enchance burrowing in silt by minute cerithiaceans.

Analysis of these and other shell features in fossils permits paleoecological inferences about the life style and role of gastropods in the marine communities of ancient seas. The four topics summarized above are important components of the answer to the question, How do architecture and construction of the gastropod shell meet the snail's structural housing needs and adapt it to the environmental demands of its habitat?

FORM, FUNCTION, AND EVOLUTION OF GASTROPOD FILTERS. Carole S. Hickman, Department of Paleontology, University of California, Berkeley.

Filters, porous structures that separate particles from fluids, vary in form and function in marine organisms that regulate flow of the medium in which they live. Filtration in mollusks has been treated primarily as a feeding adaptation, and it is normally associated with bivalves.

However, biological filters serve functions that are not necessarily related to capturing food particles and have evolved along several different lines in marine prosobranch gastropods. Examination of the construction and function of man-made filters provides some general principles that help us understand gastropod filters: (1) filters are not necessarily sieves—a sieve is one kind of filter; (2) filters tend to become clogged; (3) a clogged filter must be replaced or cleaned if it is to maintain functional efficiency; (4) filtering systems frequently involve a series of filters of different mesh sizes; (5) filters have a built-in resistance to the flow of fluids through them; (6) filters can be used either to select desirable particles or to exclude undesirable ones; (7) there are different designs or filter morphologies that can accomplish the same task—some filters are built to get by while others are more elaborate, perhaps for functional reasons other that filtration.

Sieving as a means of particle capture is not easy to document in gastropods. The mucus filtration nets produced by gastropods in the family Vermetidae are not sieves. They are sticky filters that are eaten along with the particles that collect on the filtration elements and repeatedly replaced or recreated. The gastropod ctenidium appears to act as a filter, although the principles involved in particle capture are, again, not demonstrably sieving. Structures that do qualifity as sieves are frequently located "upstream" from the ctenidium. They function to exclude undesirable particles rather than to select desirable ones, and they are highly variable in their form and construction. Some are elaborations of mantle tissue, as in the Turritellidae, while others are constructed from epipodial tissue, as in the Trochidae.

The most elaborate exclusion filters are on the enrolled incurrent "epipodial siphons" that have evolved independently several times in fully infaunal lineages in the trochid subfamily Umboniinae, notably in *Umbonium* Link and *Bankivia* Menke. In *Umbonium*, two major constructional problems of filters are overcome: (1) spacing in the filtration mesh is adjustable so the rate of flow and particle size can be regulated, and (2) they are self-cleaning through incorporation of a cephalic tentacle that removes particles clogging the mesh. Grades of evolution in trochid exclusion filters are poor indicators of relationships but good predictors of life habits and function.

HYDROTHERMAL VENTS, SULFIDE SEEPS AND MOL-

LUSKS. Ruth D. Turner, Harvard University, Cambridge, Massachusetts.

Mollusks are among the most conspicuous members of the lush deep-sea communities surrounding hydrothermal vents, such as those of the Eastern Pacific, and sulfide seeps, like those found off San Clemente, California and in the Gulf of Mexico at the base of the Florida Escarpment off Tampa, Florida. Numerous independent studies of these communities, since the first one was discovered in 1977, have shown that the base of the food chain at these sites is chemosynthetic bacteria. These bacteria oxidize the sulfide compounds, particularly hydrogen sulfide (H_2S), emanating from the vents or seeps and utilize the energy released to transform carbon dioxide (CO_2) in the water to organic carbon. It has also been shown that, though the vents and/or seeps may be widely separated, these sulfide based communites, found at depths ranging from about 2000 to 4000 meters, have similar faunas. The characteristic mollusks of these communities (e.g. vesicomyid clams, mytilids, patelliform and trochiform archaeogastropods) are not distributed generally throughout the deep-sea benthos becoming abundant and large around the vents and seeps, but rather are restricted to the vicinity of them. The origin, evolution and systematic relationship of these molluscan species, their modes of feeding and reproduction, means of dispersal and their relationship with other members of the community are still not fully understood. This is particularly true of the seep communities off Tampa, Florida. These, the most recently discovered of the deep-sea sulfide based communities are also the most isolated and the first known from the Atlantic.

COMPARATIVE REPRODUCTIVE BIOLOGY OF *PLANAXIS* SPECIES. Richard S. Houbrick, Smithsonian Institution, Washington, DC.

The Planaxidae comprise a number of species and genera that brood their eggs in unique specialized incubatory pouches formed by ectodermal invagination in the head-foot. Members of various genera release larvae at different growth stages. Nearly all kinds of developmental modes are found among genera and poecilogony has been documented in one species.

HIGHER CATEGORY RELATIONSHIPS AMONG TRICULINAE (GASTROPODA) FROM CHINA: NEW GENERA, PHENETICS, CLADISTICS AND BIOGEOGRAPHY. George M. Davis, Academy of Natural Sciences of Philadelphia, Pennsylvania, and **Yuan-Hua Kuo,** China National Centre for Preventive Medicine, Shanghai, China.

A new genus of Triculinae was discovered in Yunnan, China. A multivariate analysis, including principal component analysis, was done to assess its relationship to potentially closely related triculine genera. Cladistic analyses included a non-computer mediated set-theory solution and computer mediated phylogenetic analysis using parsimony (PAUP). Phylogenetic and biogeographic implications of the data relative to the direction and tempo of the evolution of the Triculinae have been examined.

ABSTRACTS
CONTRIBUTED PAPERS

THE PLIOCENE MOLLUSK FAUNA OF VIRGINIA. Lyle D. Campbell, University of South Carolina at Spartanburg, Spartanburg.

Pliocene age (3.5 to 2.5 million years bp) fossiliferous deposits underlie much of the Virginia Coastal Plain, and are frequently exposed in stream and river banks and in sand and gravel pits. Mollusk-dominated biotas characterize the three biostratigraphic units present: the lower, or zone 1 Yorktown (97 mollusk species); upper, or zone 2 Yorktown (509 mollusk species), and the Croatan (108 mollusk species). Adjusting for overlap, I have monographed 575 valid mollusk species and subspecies including a new genus, *Juliamitrella* (Columbellidae), a new subgenus, *Odostomia* (*Chesapeakella*) (Pyramidellidae), 74 new species and subspecies, and two replacement names.

Zone 1 faunas are typical of a cold temperate open shelf, and are often poorly preserved. Zone 2 habitats include sound, estuary, near shore, open shelf, shell-reef, and high and low energy environments. Preservation of zone 2 faunas is good to exceptional. Taken collectively, the zone 2 faunas reflect warm temperate conditions not presently found in the Western Atlantic. Croatan faunas indicate near shore, fresh water, and estuarine habitats, and the fossils commonly show physical abrasion and chemical deterioration.

Yorktown and Croatan species are especially important for evolutionary studies of the recent Western Atlantic fauna. Additionally, the holotypes of a a surprising number of common recent species were originally described from the Yorktown Formation.

Systematic analysis of the Virginia Yorktown and Croatan faunas has been hampered by a general lack of available literature, most of the significant literature being over a century old, and by the formidable numbers of species. Including synonyms, homonyms, dubious, and rejected species, over 2000 names have been proposed or cited in the Yorktown and Croatan literature.

MOLLUSCS AND THE ORIGIN OF EL NIÑO. Harold B. Rollins, Department of Geology and Planetary Science, University of Pittsburgh, Pennsylvania.

Marine bivalves and gastropods recovered from archaeological sites in the Santa and Chao river valleys, just north of Chimbote, north-central coastal Peru, suggest a major change in the structure of the East Pacific water mass about 5000 years B.P. In this region the present-day cold water (Peruvian Province) molluscan species are found in archaeological shell middens yonger than about 4300 years B.P. whereas older sites contain warm-water (Panamic Province) species. The modern boundary between the two faunal provinces is at about 5°S latitude, 400 kilometers north of the Santa and Chao valleys. *In situ* molluscan beach associations with multiple-year age classes also occur at the sites, ruling out the possibility of a short-term thermally anomalous molluscan assemblage (ala Zinsmeister, 1974), such as might occur with sporadic El Niño events. The high diversity of Panamic species also supports a major water mass change. Corroborating evidence can be seen in the age and distribution of land-based phosphate deposits, beach ridges, diatom and radiolarian assemblages, as well as the temporal pattern of glacial advance and retreat. The reorganization of the water mass off north-central Peru probably signals the origin of El Niño perturbations, as the latter would only be possible following the northward extension of the cold Humboldt current and coastal upwelling. Immediately prior to about 5000 years B.P., the coastal desert of Peru did not exist and pre-ceramic populations of hunter-gatherers were probably less dependent upon a maritime food base of molluscs and fishing (e.g., anchovetas) than has been previously postulated.

THE APLACOPHORAN FAMILY PROCHAETODERMATIDAE, Amelie H. Scheltema, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

Species of Prochaetodermatidae are among the most numerous benthic animals in some deep-sea, soft-bottom localities, including the North American Basin and Aleutian Trench. The single named genus and three additional, presently recognizable, unnamed genera occur in both the North and South Atlantic Ocean; at least two are found in the eastern Pacific as well. The six species in three genera considered vary in geographic range from wide-spread to narrowly distributed. Genus membership is determined by spicule morphology.

STUDIES ON THE BIOLOGY OF THE ABALONE *HALIOTIS ROEI* ON BEACHROCK PLATFORMS IN THE METROPOLITAN AREA OF PERTH, WESTERN AUSTRALIA. Fred E. Wells, Western Australian Museum, Perth 6000, Western Australia.

In the late 1960's a fishery for the abalone *Haliotis roei* (Gray, 1827) was developed along the central west coast of Western Australia. The fishery produces about 100,000 kg of abalone annually, with much of the catch coming from beachrock platforms in the Perth metropolitan area. Increasing pressure on abalone stocks, largely by amateur fishermen, led to a temporary closure of the metropolitan fishery in March 1982; the closure is still in effect. In November 1982 a three year research programme on the fishery biology of *H. roei* was begun to develop information necessary for sound management of the fishery. The central effort is devoted to a two year study of monthly variations in gonad condition and food consumed by *H. roei* on three metropolitan platforms. Associated information such as size at maturation, fecundity, sex ratios, feeding strategy, growth and habitat preferences is also being developed.

FUNCTIONAL MORPHOLOGY AND HISTOCHEMISTRY OF THE ATTACHMENT THREAD OF THE ECTOPARASITE *BOONEA* (= *ODOSTOMIA*) *IMPRESSA* (GASTROPODA: PYRAMIDELLIDAE). J. Evan Ward, University of Delaware, College of Marine Studies, Lewes.

Secretion of an attachment thread by the ectoparasite *Boonea* (= *Odostomia*) *impressa* (Say, 1821) used to secure itself onto the shell of a host, *Crassostrea virginica* (Gmelin, 1791), was observed under laboratory conditions.

Scanning electron and light microscopy revealed that the thread is a tri-filamentous structure, comprised of two functionally distinct subunits running parallel along a central axis. Two elastic, coiled subunits and one plastic, striated subunit function complementally to form a resilient thread. The two coiled subunits exhibit elastic deformation, while the striated subunit exhibits plastic deformation.

Histochemical tests indicated that both types of subunits are proteinaceous, and a thin membrane enveloping the subunits contains acidic carbohydrates.

A PARTIAL DESCRIPTION OF THE ANATOMY OF *PLEIOPTYGMA HELENAE* (GASTROPODA: NEOGASTROPODA). James F. Quinn, Jr. Academy of Natural Sciences, Philadelphia, Pennsylvania and **William G. Lyons** Florida Department of Natural Resources, St. Petersburg.

The neogastropod genus *Pleioptygma* Conrad, 1863, is represented by several Tertiary species, but only one Recent species, *P. helenae* Radwin and Bibbey, 1972. Shells of this species, usually inhabited by hermit crabs, are uncommonly collected in lobster traps off the Carribean coast of Honduras and Nicaragua. Dissection of the anterior part of the animal of the only live-collected specimen yet known revealed a suite of characters which partially clarify the systematic position of the genus.

Externally the animal has a large, very muscular foot, a thick, muscular siphon, and a thin mantle with a narrow band of muscle along the edge. The mantle cavity contains a small head with a conical snout and rather short cephalic tentacles, the eyes located about midlength, a large dorsoventrally flattened penis, and a large hypobranchial gland. A fragment of the ctenidium was preserved and has rather long filaments. Neither osphradium nor intestine was preserved. Internally, only the anterior portion of the foregut was preserved. The proboscis is very long, with three major morphological divisions: 1) an anterior supporting tube or sheath; 2) a large, very muscular buccal sac; and 3) a very long tube running through both 1 and 2, forming the major extensible length of the proboscis. The buccal mass lies just posterior to the proboscis complex and contains the radula sac. The radula is triserial; all three teeth in a row are broad, comb-like laminae. The unpaired foregut gland has a long duct and lanceolate, muscular bulb.

Pleioptygma has been assigned to either the Mitridae (*sensu lato*) or the Volutidae by various authors. However, the unique configuration of the foregut precludes inclusion of *Pleioptygma* in either of these families, or in any other described neogastropod family. Therefore, a new family is required for *Pleioptygma*. Affinities of this genus are unclear, although we suggest derivation from an ancestor in common with the Mitridae.

TAXONOMY AND BIOGEOGRAPHY OF DOMINICAN REPUBLIC NEOGENE TURRIDAE (NEOGASTROPODA).

Matthew J. James, Department of Paleontology, University of California, Berkeley.

Numerous excellent outcrops of three fossiliferous formations occur along river drainages in the Cibao Valley of the northern Dominican Republic. Abundant material from the Cercado, Gurabo, and Mao Formations was collected by a Swiss-organized and -funded project headquartered at the Naturhistorisches Museum in Basel and by the dilligent efforts of Harold and Emily Vokes of Tulane University. This material, along with additional specimens collected by me in July 1983, and fossil type material from several museums, constitutes the basis for a taxonomic revision of the neogastropod family Turridae from the Dominican Republic. The Dominican Republic turrid fauna is extremely well preserved, abundant, and diverse and provides a basis for examining interacting patterns of taxonomic, biogeographic, and evolutionary complexity. Several taxonomic studies of Dominican Republic turrids appeared between 1849 and 1922, but few studies have appeared in the last 60 years. Pioneering taxonomic work by Guppy, Gabb, Dall, Pilsbry, Maury, Woodring, and others, has provided the foundation on which the present work is based. However, most of this previous work represents post-Darwinian pre-New Synthesis taxonomic procedures and does not incorporate recent conceptual advances. Increased sample sizes for all taxa allow resolution of problems involving intraspecific and interspecific variation. Geographic and stratigraphic variation also contribute to the larger taxonomic structure of the fauna. The turrid fauna has widespread biogeographic affinities. Species recognized from the fauna also occur as fossils in Jamaica, Trinidad, Venezuela, Ecuador, Panama, Costa Rica, Mexico, and the southeastern United States. Resolution of this pattern is best explained thorugh dispersal of planktonic larvae rather than through a vicariant event. Aspects of the generic and subfamilial classification schemes currently applied to Recent members of the family Turridae are also considered. This fauna represents an intermediate stage in the evolutionary modernization of worldwide Neogene turrid faunas from older Paleogene faunas.

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FOSSIL AND RECENT *MICRARIONTA* ON SAN NICOLAS ISLAND, CALIFORNIA.

Timothy A. Pearce, Department of Paleontology, University of California, Berkeley.

Micrarionta sodalis (Hemphill, 1901), extinct, and *M. opuntia* Roth, 1975, extant, are land snails endemic to San Nicolas Island, the farthest offshore of the southern California Islands. Sedimentary deposits including abundant land snail fossils from the late Pleistocene to the present provide an ideal situation in which to examine changes in shell morphology through time and the evolutionary relationship between the two species of snails. Shells of the two species are morphologically similar, but distinct, differing principally in adult size, and subtly in other characters including greater umbilical diameter, lip width, shell thickness, and parietal callus thickness in *M. sodalis*. Mean diameter of *M. sodalis* is 11.8 mm and that of *M. opuntia* is 8.4 mm. A preliminary examination of shell size shows no overlap in diameter of the two species, and suggests that diameter of *M. sodalis* remained essentially constant from the time of the snail's appearance to its extinction. *M. sodalis* occurs in a variety of deposits from 127,000 or more years old, to Native American middens fewer than 7,000 years old. *M. opuntia* is found in more recent sediments. The two gastropod species appear to have coexisted only briefly in the geologic history of the Island. Changes in climate or vegetation, Native American activity, or competition between the two species, may have played roles in the extinction of *M. sodalis*. Morphological comparisons within *Micrarionta* will help to determine whether *M. opuntia* evolved in place from *M. sodalis* or originated from one of the four other southern California Islands where the genus is endemic.

NEST BUILDING OF *COCHLOSTYLA PITHOGASTER* (FERUSSAC) (PULMONANTA; BRADYBAENIDAE).

Kurt Auffenberg and **Garth Auffenberg,** Florida State Museum, University of Florida, Gainesville.

Extensive studies on *Cochlostyla* (*Orthostylus*) *pithogaster* (Ferussac) from 1981 to 1983 have yielded many interesting aspects of its life history. One of the most fascinating is the species' nest building behavior, which it shares with at least one species of the subgenus *Hypselostyla* and one species of the related genus *Calocochlea*.

The few published reports on the nest building of arboreal snails deal with species which lay their eggs in or on the ground, much like non-climbing species. *Cochlostyla* (*Orthostylus*) *pithogaster* (Ferussac), *Cochlostyla* (*Hypselostyla*) *carinata* (Lea) and *Calocochlea caillaudi* (Deshayes), and perhaps the entire Heliocostylinae, are unique in the cementing together of living leaves during nest construction.

Thirty three nests of *Cochlostyla pithogaster*, four of *Calocochlea caillaudi* and one of *Cochlostyla carinata* were examined. Although nests of *C. pithogaster* were found in at least nine tree and vine species, 78% of the leaves utilized had lengths two times greater than the width. One to three leaves are used for each nest. Nest construction and egg laying occur simultaneously as the snail moves backwards towards the leaf tip(s) depositing eggs in the cavity formed by the pulling and cementing together of the leaf margins.

The first and last groups of eggs laid are small, misshapen and inviable. These dry and form upper and lower plugs which presumably protect the viable eggs from dessication.

The nests of *Calocochlea caillaudi* were virtually identical to those of *Cochlostyla pithogaster*. Although the one examined nest of *Cochlostyla carinata* differed substantially, no conclusions should be drawn, due to the observed variability in the nests of the other species. With further study this unique nest building behavior may prove to be of taxonomic significance.

A COMPARATIVE STUDY OF SHELL SHAPE IN FOUR POPULATIONS OF *CAMPELOMA* (GASTROPODA: VIVIPARIDAE). **M. Bowie Kotrla** and **B. J. Dougherty,** Department of Biological Science, Florida State University. Tallahassee.

Shell morphometrics have often been used to analyze the ontogenetic and phylogenetic relationships of molluscs. Among gastropods, biometric data may be particularly useful for groups in which other reliable conchological features are lacking. The genus *Campeloma* has long been considered such a group (Clench, W. J., 1962. Occ. Pap. Moll. 2:261–287).The objective of this study was to determine whether easily measurable parameters can be used to discriminate among sexes or populations of *Campeloma.*

Sexually reproducing diploids, *C. geniculum* (Conrad, 1834), were collected from the main channels of the Ochlockonee and Suwanee rivers in north Florida. *Campeloma parthenum* Vail, 1979, a triploid parthenogen, was collected from Lake Talquin in the Ochlockonee drainage system. An additional group of triploid parthenogens, putatively *C. geniculum*, was collected from the Withlacoochee River in the Suwanee drainage.

Shell length and six other linear dimensions were measured on shells of 50 individuals of each sex from each locality and transformed to log 10. Shape variables of the form logX—logY, which, under the lognormal assumption can be analyzed by parametric statistical tests, were created from the above size variables.

The results show that length is a reliable indicator of shell size in spite of variable erosion of the apex, and that diploid females are larger then males in most dimensions. Regression analysis of the diploid populations indicates that the Suwanee River individuals are more globose than those from the Ochlockonee River. Although males from the two localities exhibit few significant differences from each other, there is a significant shape difference between the two groups of females.

The growth patterns of the triploid parthenogenetic females are similar to those of diploid males and females. Withlacoochee River parthenogens exhibit a shape resembling that of sexually reproducing females, but Lake Talquin parthenogens do not. This result supports the recognition of *C. parthenum* as a distinct species.

COMPARATIVE LIFE HISTORY PATTERNS WITHIN A LAKE LITTORAL ZONE SNAIL COMMUNITY. **Eileen H. Jokinen,** Ecology Section, U-42, The University of Connecticut, Storrs.

Life cycles of thirteen species of aquatic snails were analyzed to determine the timing of reproduction within the littoral community of a small, shallow, highly eutrophic lake in southern New England. The timing and duration of oviposition and juvenile recruitment varied considerably between species. Four species (*Amnicola limosa, Helisoma campanulatum, H. anceps, Laevapex fuscus*) had a well-defined annual life cycle; three species (*Gyraulus circumstriatus, Physella ancillaria, Fossaria modicella*) had almost continual recruitment from spring through autumn; and six species (*Pseudosuccinea columella, Gyraulus deflectus, Micromenetus dilatatus, Promenetus exacuous, Planorbula armigera,* and *Ferrissia fragilis*) had two or three well-defined reproductive periods per year. Closely related species tended to differ the most in their reproductive periods and/or duration of oviposition. The division of the reproductive season (April through November) in Roseland Lake may act to reduce interspecific seasonal variation of dietary resources (detritus, diatoms, green algae, etc.).

ARTIFICIAL INTRODUCTIONS USED TO ASSESS GENE FLOW POTENTIAL WITHIN AND BETWEEN POPULATIONS OF THE FRESHWATER SNAIL, *GONIOBASIS PROXIMA*. **Robert T. Dillon Jr.,** College of Charleston, South Carolina.

Dillon and Davis have described an unusual race of *Goniobasis proxima*, race *B*, that inhabits water much harder than the typical races *A* and *C* and has an unusual shell morphology. In July, 1979, a series of 12 transplant experiments were initiated involving race *B* and three other populations of *G. proxima* from softer water. At each site, 500 native snails were removed and replaced with 500 snails from a second population fixed for some unique allele at one or two enzyme loci. The sites were resampled in 1983, using starch gel electrophoresis to identify populations where the introduced genomes had in fact become established.

None of the six introductions involving race *B* snails was successful, although two involving races *A* and *C* snails succeeded. Introduced genes have spread long distances at these two sites, about 15–20 meters per year upstream and 5–10 meters per year downstream. Even though they were born in a foreign environment, snails homozygous for the introduced genotype retained the shell shape (not size) of their parents.

Coyner Springs is a hardwater spring near Waynesboro, Virginia, 100 miles north of the normal range of *G. proxima*. In July, 1980, 1100 *G. proxima* were introduced, half belonging to the hardwater race *B* and the other half from a race *A* population native to a typical softwater stream. Both populations survived well, and new generations of snails have been born every spring since the introduction. However, electrophoretic analysis completed in 1983 confirmed that only race *B G. proxima* have reproduced in the hard waters of Coyner Springs. One living member of the race *A* parental stock was identified, apparently healthy after three years in hard water. The inability of race *A* snails to reproduce in hard water suggests, however, that the races may be reproductively isolated.

METABOLIC RESPONSES TO TEMPERATURE BY PLEUROCERID SNAILS FROM THE INTERIOR HIGHLANDS.

Mark E. Gordon, Department of Zoology, University of Arkansas, Fayetteville.

Lotic systems within the Interior Highlands physiographic region of the central United States are typically spring-fed habitats with distinct riffle-pool fluvial geomorphology. Generally, streams of similar latitude exhibit annual thalweg temperature extremes from 0°–35°C. Interactions of groundwater input with flow dynamics, depth, and isolation produce Interior Highlands streams that are temporally and spatially of moderate temperature and/or thermally patchy.

Three pleurocerid snails from this region—*Elimia potosiensis* (Lea), *Leptoxis arkansensis* (Hinkley), *Pleurocera acuta* Rafinesque—were maintained at four temperatures (2°–32°C) within the annual thermal range for regional streams 7–10 days prior to respiration determinations. Rates were obtained for these temperatures and ± 10°C acute temperatures within this range. *Elimia* exhibited some ability to acclimate thermally as indicated by high Q_{10}'s and translation, especially between 12°–22°C acclimation groups. *Leptoxis* exhibited limited acclimation with high Q_{10}'s and translation between 12°–22°C acclimation groups. However, this response was limited to the 22°C determination temperature. *Pleurocera* acclimated throughout the experimental regime except at the lower extreme.

All three species had depressed rates at 2°C with *Elimia* and *Leptoxis*, Interior Highlands endemics, also depressed at 32°C indicating lack of metabolic homeostasis regulation at these extremes. Data suggest critical thermal maxima for *Elimia* and *Leptoxis* near 32°C and 28°C, respectively. *Pleurocera* rates continued to increase with elevation from 22°–32°C, reflective of a considerably higher critical thermal maximum. Geographic distributions correlate with these observations. *Pleurocera* ranges from southern Canada to Louisiana and, accordingly, possesses considerable thermal acclimatory ability. *Elimia* is restricted to the thermally moderated streams of the Interior Highlands, acclimating only to a middle range of temperatures. *Leptoxis* is restricted to only a few spring-dominated systems and is rather stenothermally adapted with acclimation only to the upper extreme of its thermal range.

REPRODUCTIVE EFFORT IN FRESHWATER PISIDIID CLAMS.

Carl M. Way, Department of Natural Sciences, Alderson-Broaddus College, Philippi, West Virginia.

One aspect of demographic theory is that life history traits are optimized by maximizing fitness under demographic selection such that a high reproductive effort (high *r*) is usually associated with a short lifespan and, conversely, a low reproductive effort (low *r*) is associated with a longer lifespan. In this report I reevaluate this conclusion utilizing life history and population energetic data from 11 species (17 populations) of freshwater bivalves of the family Pisidiidae. Reproductive effort (Re:P × 100) varies considerably in this family (range: 5–35%), both at the intra- and inter-specific level. There is no significant difference between the reproductive efforts of semelparous and iteroparous forms. In addition, embryonic development and adult growth often occur simultaneously in these forms. A demographic tradeoff between reproductive effort and lifespan seems paradoxical in this context, considering that lifespans for many pisidiids remain close to one year regardless of their reproductive effort. There is no significant correlation between lifespan and Re: P or between age at first reproduction and Re: P for the species considered. However, Re: P does exhibit significant correlations with size at maturity, maximum adult shell length, and number of young per brood. Production efficiency (P:A × 100) is significantly correlated with both lifespan and maximum adult shell length, but not with Re: P. These data support the conclusions of Way (1983) that reproductive effort and the life history traits of the Pisidiidae are probably determined by a combination of: 1) allometric constraints on reproduction such that reproductive output is directly proportional to clam size; and 2) cumulative exposure to localized environmental factors that variously affect the physiological processes of clams of different sizes and of clams born at different times of the year.

CORBICULA FLUMINEA (MÜLLER) (MOLLUSCA: BIVALVIA: CORBICULIDAE) IN LAKE WACCAMAW, COLUMBUS COUNTY, NORTH CAROLINA, ITS DISTRIBUTION, DISTRIBUTIONAL ECOLOGY, AND GROWTH.

Hugh J. Porter, University of North Carolina, Morehead City.

The *Corbicula fluminea* population in Lake Waccamaw was intensively studied during 1979–1981. During this period small *Corbicula* (≥ 3 mm length) were found throughout the lake, but larger *Corbicula* (≥ 3 mm length), were generally restricted to a shallow, low-organic, sandy substate zone in the northwestern half of the lake, an area in which the emergent plant Spatter-dock (*Nuphar luteum* Sibth. & Smith) also seems restricted. No significant correlations were observed between densities of either of the two sizes and any of the endemic molluscs within the lake. Three different yearclasses are believed to have been observed during the period.

ASSESSING EFFECTS OF ENVIRONMENTAL PERTURBATION THROUGH ANALYSES OF *CORBICULA* (CF *FLUMINEA*) SHELL MICROSTRUCTURE.

Lowell W. Fritz and **Richard A. Lutz,** Department of Oyster Culture, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, New Brunswick.

Anthropogenic and natural seasonal environmental perturbations were reflected in shell growth patterns of specimens of *Corbicula* cf *fluminea* living at the northernmost extent of their range along the east coast of North America (Raritan River, NJ). The growth of organisms in experimental cages was monitored during 1981 (August 1981–January

1982) and 1982 (July–December) at stations located upstream (controls—2 stations) and immediately downstream (perturbed—1 station) from a combined industrial-sewage effluent. In 1981, the growing shell margin of each clam was notched with a small drill before each was placed in a cage; these marked organisms were sacrificed after various lengths of time. In 1982, specimens were not notched, but a growth cessation mark present in all caged organisms marked the beginning of the monitored growth period in shell microstructure. Individual shell valves were imbedded in epoxy resin and radially sectioned. Acetate peels and polished thin sections were prepared using standard techniques. Microgrowth increments in the outer crossed-lamellar layer were deposited at an average rate of one increment per day. Furthermore, a growth discontinuity in the inner complex crossed-lamellar layer and an associated growth cessation mark in the outer layer resulted from the discontinuance of growth in winter. Based on increment counts, growth resumed in late March or early April each year as water temperatures rose above approximately 10°C. Growth rates during spring and early summer averaged 65 and 45 μm/increment in 1981 and 1982, respectively. A growth cessation mark found in all specimens sampled in 1981 ($n = 53$) was dated to within two days of a major storm using increment counts, revealing the accuracy of their use to date the formation of shell regions.

There were no significant differences in growth rates or shell growth patterns among specimens (eventually collected from cages at the three stations) in the period from spring to the beginning of the monitored growth period each year. In 1981, growth rates of specimens at each site were significantly slower during the monitored growth period than before it; this was most likely a result of injury inflicted by notching the ventral shell margin. However, unnotched specimens moved to the perturbed site in 1982 subsequently grew at significantly slower rates during the monitored period than those collected from cages at the control sites. Analyses of radial shell sections of specimens collected from the natural population at one of the control stations in 1982 revealed no significant differences in microstructural growth between these specimens and those from cages at both control stations.

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AMMONIUM EXCRETION BY THE ASIATIC CLAM *CORBICULA FLUMINEA*. **Diane D. Lauritsen,** North Carolina State University, Raleigh.

Ammonium excretion rates of *Corbicula fluminea* freshly collected from a eutrophic, coastal North Carolina river vary seasonally, with highest rates in summer. In areas of the river where they are abundant, clam excretion could supply from one-third to one-half of summer phytoplankton uptake of ammonium, when allochthonous loading to the river is at a minimum. Laboratory experiments show that with increasing food concentrations clams are ingesting increasingly more algal nitrogen, but ammonium excretion rates are highest at lower food concentrations. This suggests that at higher food concentrations, a greater percentage of nitrogen ingested will be found in the clam's feces.

COMPARATIVE STUDY OF THE DIGESTIVE GLAND AND TERTIARY DIGESTIVE TUBULE MORPHOLOGY IN *POLYMESODA CAROLINIANA* AND *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE). **Kashane Chalermwat,** Department of Biological Sciences, University of Southern Mississippi, Hattiesburg.

Changes in digestive tubule morphology through time in two species of corbiculid bivalves, *Polymesoda caroliniana* (Bosc) and *Corbicula fluminea* (Müller), have been examined. Hourly samples were taken of the bivalves in their natural habitat throughout a 24 hour period. The animals were fixed in the field and later sectioned and stained for histological analysis. Three individuals of *P. caroliniana* were sampled every hour from an exposed brackish water marsh population in Ocean Springs, Mississippi in April 1984. Twelve to sixteen individuals of *C. fluminea* were sampled hourly from Talahalla Creek, Mississippi in July 1984. Sections of the digestive gland of the two bivalves reveal morphologically similar tertiary tubules. However, the gland of *P. caroliniana* is larger and more compact than that of *C. fluminea*. Throughout the sampling period three types of tubules were found in *P. caroliniana*. The first had large and prominent excretory vacuoles; this type was dominant in every sample. The second type had less distinct excretory vacuoles in the cell cytoplasm; this type was less abundant than the former, but was consistently found in every sample. The third type was rarely found in individuals; it was, however, found scattered through the sampling period. Similar results were obtained for *C. fluminea*; three tubule types were found. Like *P. caroliniana* individuals would have the gland dominated by either the tubule type with excretory vacuoles, the type with less distinct excretory vacuoles, or the type without. In individuals of both species with excretory vacuoles, the vacuoles were present in tubules of varying morphology, ie. those with star shaped lumens, wide oval lumens, and tubules that had the distal tips of the digestive cells breaking off into the lumen. From the presence of excretory vacuoles in individuals of the two species throughout the light-dark period it seems that both bivalves are continuous feeders exhibiting continuous digestion.

ON RADULAR TEETH OF SOME BRASILIAN PROSOBRANCHS, **E. C. Rios** and **Iara S. Calvo,** Museu Oceanografico da FURG RS, Brasil.

During the preparation of the junior author's master's thesis, we observed the radular teeth of some Brazilian Prosobranch species, as follows:

a) For the first time, we studied the radulae of *Pleurotomaria atlantica* (Ricos and Mattews, 1968) which is of the hystrichoglosse type; *Solariella carvalhoi* which is rhipidoglossate having the following formula: 12.3.R.3.12.; and *Typhina riosi*.

b) Watson described *Trophon acanthodes*, (Challenger Reports, 1882), from Argentine waters. Carcelles (1947) removed this species from *Trophon* to the genus *Fusus*. Rios (1975) named it *Fusinus acanthodes*. Observing the radula we note that it is of trophonoid type and due to the long siphonal canal, we suggest inclusion in the subgenus *Pagodula* Monterosato, 1884. The present "status" would thus be *Trophon* (*Pagodula*) *acanthodes* (Watson, 1882). Besides that we extracted the radula of *Lyria guildingii* (soft parts unknown according to Weaver and Du Pont, 1970) which is completely different from the genus type. It was not possible to include this species within any genus of the Volutidae family.

c) Abbott and Dance (1982) synonymized *Buccinanops* with *Bullia* (Family Nassariidae). Studying the radula, we verified that the rachidian teeth cuspids of *Buccinanops* decrease in size toward the ends and the lateral teeth are multicuspidate. On the other hand, in *Bullia* the rachidian teeth cuspids have the same size and the laterals are bicuspidate. Also, the same authors (1982) placed *Thais nodosa meretricula* under the genus *Purpura*. Comparing the radula we observed they are also different, especially the *Purpura* rachidian central cuspid, which is very long.

WHELK FISHERY IN THE SOUTH ATLANTIC BIGHT: PRELIMINARY OBSERVATIONS. Arnold G. Eversole, Department of Aquaculture, Fisheries and Wildlife, Clemson University, South Carolina and **William D. Anderson,** Office of Conservation, Management and Marketing, South Carolina Wildlife and Marine Resources Department, Charleston.

Poor shrimp harvests in the South Atlantic have led to a diversification of the commercial shrimp fleet. Two commercial shrimp fishermen began to fish sublittoral populations of whelks (*Busycon carica* and *B. canaliculatum*) in the spring of 1978. Since that time, the number of licensed fishermen has increased from 2 to 70 and the landings from several thousand bushels to 32,567 bushels in 1982 and 28,353 in 1983. Considerable concern has been voiced about maintenance of the resource in light of increased exploitation since only 5% of available licensed trawlers have applied for whelk fishing licenses. A research program was initiated to gather information on the fishery and the species being harvested.

Currently, only commercial shrimp trawlers fish for whelks. Smaller boats use crab scrapes while larger vessels drag nets with 4-inch stretch mesh (84 twine) and ⅝" ticker chains to catch partially buried whelks. The fishing season usually extends from February to May, traditionally a closed shrimping period. Catches sometimes exceed 100 US bushels per day and 10 US bushels per hour. Preliminary results for 1984 indicate an average US bushel contained 107.4 whelks with approximately 89% being *B. carica* and 11% *B. canaliculatum*. Rarely were *B. spiratum* and *B. contrarium*, the two other species found in South Carolina waters, found in the catch. Average shell length of *B. carica* and *B. canaliculatum* was 133.6 and 135.3 mm, respectively. Female *B. carica* were significantly larger (P 0.05) than male *B. carica* and more abundant in the catch. Size selective harvesting techniques and a 4½-inch minimum size partially explain the disparity in the sex ratio.

Heat and pressure is applied to large containers of harvested whelks to facilitate hand shucking. Shucked meats, which are predominantly the head-foot portion of the whelk, contain mostly protein (74%) with lower levels of ash, fat and carbohydrates (8%, 3%, and 15%, respectively). Some meats shucked in South Carolina are shipped on ice to the northeastern United States for canning or sale in retail fish markets while others are frozen and transported to the Orient.

A mark-recapture study was initiated to estimate growth, movement and population density. To date, 8,234 whelks have been marked and 369 have been recaptured. Commercial fishermen have returned approximately 80% with the remainder being returned by the general public. A reward system and high profile publicity campaign assisted the recapture program. Although observations from these returns indicate that growth is very slow and movement limited, studies are continuing to provide size-specific growth rates, movement to and from estuarine areas and estimates of population density in exploited areas.

A MIDDLE-AMERICAN LAND SNAIL FAUNA FROM THE EOCENE-OLIGOCENE OF TEXAS. Barry Roth, Museum of Paleontology, University of Califorrnia, Berkeley.

An undescribed large helminthoglyptid snail of the genus *Lysinoe* occurs in the Colmena Tuff and Chambers Tuff on the Vieja Group, Presidio County, Texas, associated with vertebrates of the Candelaria and Porvenir local faunas. It is also present in correlative strata in Brewster County, Texas, and in a predominantly marine sequence in Nuevo Leon, Mexico, associated with a "Vicksburg" molluscan fauna. The vertebrate assemblages belong to the Uintan and Chadronian North American Land Mammal "Ages." Radioisotopic dates indicate a time span of about 41–38 Ma before present. The species closely resembles Recent *Lysinoe ghiesbreghtii* from southern Mexico and Central America. Climatic and ecological parameters from the range of *L. ghiesbreghtii* imply that conditions in this part of Texas during the late Eocene-early Oligocene were moist and temperate; the prevailing vegetation was probably an ecological analogue of the seasonal temperate forests of present-day Chiapas, Mexico. Mean annual rainfall in excess of 123 cm, either with or without a winter dry season is indicated. Many plant species of temperate Mexican forests have counterparts in the southeastern United States; *Lysinoe* supports the concept of a formerly continuous forest distribution around the northwestern Gulf of Mexico.

The Candelaria local fauna also includes the helminthoglyptid genus *Polymita*, now confined to Oriente Province, Cuba. Other land snails from the Chambers Tuff include two subgenera of *Pleurodonte* (Camaenidae), now confined to Jamaica and the Lesser Antilles, and *Xerarionta* (Helminthoglyptidae), now living from southern California to southern Baja California. *Polymita* and *Pleurodonte* both now inhabit more tropical forests than *Lysinoe*. *Xerarionta* inhabits arid and semiarid zones within the influence of Pacific fog. Climatic equability may have permitted to co-occurrence of genera that now show conflicting climatic preferences. The snail assemblages document a southward retreat of land mollusk genera through the Tertiary and a developing allopatry.

PRELIMINARY OBSERVATIONS ON *HELMINTHOGLYPTA TRASKII* AND ITS SUBSPECIES (GASTROPODA, PULMONATA). **Jane E. Deisler,** Department of Ecology and Evolutionary Biology (West), University of Arizona, Tucson.

Helminthoglypta traskii and its subspecies traditionally are defined by distributional, conchological, and anatomical characters. These snails are found in the L. A. Basin and Penninsular Ranges physiographic province of southern California, ranging from Kern County, California, southward to Santa Tomas, Baja California del Norte. They are united conchologically by the presence of the incised spiral lines on the last two whorls and by variable degrees of surface papillation. These characteristics are shared with the *H. ayersiana* series. In the past *H. traskii* and its subspecies were placed in the subgenus *Charodotes* Pilsbry, 1939, which separated these taxa from the *H. ayersiana* series which was placed in *Helminthoglypta* sensu stricto. The basis for *Charodotes* is the possession of a simple tubular penis instead of the double-tube structure found in *Helminthoglypta* s.s. However, it has been shown that the single-tube penial structure does not exist so that the two subgenera are synonymous. Preliminary anatomical studies indicate that *Helminthoglypta traskii* is characterized by the presence of a long spermathecal diverticulum, a long epiphallic caecum, a slender penis with a long double-tube portion, and an anterior saccular portion of the penis that is slender and funnel-shaped. Subspecies appear to be definable on the basis of shell characters and geographic separation, with *Helminthoglypta traskii* sensu stricto occuring in the Los Angeles Basin. Further anatomical and conchological studies are in progress.

EFFECT OF HABITAT ON SHELL MICROSTRUCTURE OF THE ATLANTIC RIBBED MUSSEL *GEUKENSIA DEMISSA GRANOSISSIMA* (SOWERBY, 1914), **Antonieto Tan Tiu,** Department of Biological Sciences, University of Southern Mississippi, Hattiesburg.

Effect of submerged habitat on the microstructure of the internal shell surface of the Atlantic ribbed mussel *Geukensia demissa granosissima* was examined. Fifty mussels of similar sizes were collected from a *Spartina alterniflora* Loiseleur-Deslongchamps marsh bed on 3 March 1984. They were marked after their wet weights and lengths were measured. Ten of each live and freshly shucked mussels were placed in cages and returned to their initial collecting site. A comparable set was transplanted to an area always submerged in water. All samples were recovered on 31 March 1984 and their wet weights and lengths were again measured. A total of 10 pairs of mussel valves from each sample (*a.* freshly shucked—3 March 1984, *b.* freshly shucked—31 March 1984 for the two sites, *c.* empty shells—31 March 1984 for the two sites) were examined by scanning electron microscopy. The remaining shells were combusted to determine organic content. Soft tissue dryweight of all mussels was also determined. Environmental data (water temperature, salinity, conductivity, dissolved oxygen, pH and sediment organic matter) were measured whenever possible on both sampling dates. Mussels in the submerged habitat had greater weight increments and dry meat to dry shell ratios than mussels in the upper marsh habitat. Scanning electron microscopy observations of the microstructure of the internal shell surface of mussels initially collected showed hexagonal tablets predominating with minimal signs of dissolution (outside the pallial line) and granular homogeneous with traces of tablets (inside the pallial line). After 28 days, mussels from the same site showed predominance of well formed hexagonal tablets with minimal signs of dissolution (outside the pallial line) and massive conglomerations (inside the pallial line). Mussels in the submerged habitat had, in addition to hexagonal tablets, many highly irregular tablets with "wrinkling" on their broad surfaces (outside the pallial line) and homogeneous to granular homogeneous to platelike formations (inside the pallial line). Further studies are needed before environmentally induced shell modification will be fully understood.

THE BERNARDINIDAE OF THE EASTERN PACIFIC (BIVALVIA). **Eugene Coan,** Department of Invertebrate Zoology, California Academy of Sciences, San Francisco.

The Bernardinidae is a family of minute, shallow-water marine bivalves as yet known only from the eastern Pacific. They combine an internal ligament with three cardinal teeth in the left valve, two or three in the right, and at least one lateral tooth. The four known species brood their young. I place the family in the Cyamiacea instead of where it has previously been placed in the Arcticacea.

In *Bernardina*, the anterior end is longer than the posterior; there is heavy concentric sculpture; and there is a large anterior lateral tooth, no posterior lateral. *Bernardina bakeri* Dall, the type species, occurs from Pacific Grove, California, to Isla Natividad, Baja California Sur. *Bernardina margarita* (Carpenter) occurs from Isla Guadalupe, Baja California Norte, to Bahía Banderas, Jalisco, Mexico. In *Halodakra,* the posterior end is longer than the anterior; the sculpture consists of fine concentric threads; and there is a posterior lateral tooth. *Halodakra, s. s.,* lacks an anterior lateral tooth. *Halodakra* (*H.*) *subtrigona* (Carpenter), the type species, occurs from Tomales Bay, California, to Mancura, Peru. A new subgenus will be proposed for *H. salmonea* (Carpenter), which has an anterior lateral tooth. This species occurs from Brookings, Oregon, to Punta San Hipolito, Baja California Sur; *Crassatella marginata* Keep and *Psephidia brunnea* Dall are synonyms.

THE GENUS *PANACCA* (BIVALVIA: PHOLADOMYIDAE) IN THE NORTH ATLANTIC. **Donald R. Moore,** Rosenstiel School of Marine Science, University of Miami.

The genus *Panacca* in the North Atlantic consists of two species, *P. africana* Fischer and *P. locardi* Dall, off the coast of North Africa, and two off the coast of North America, *P. arata* Verrill and Smith and *P. fragilis* Grieg. All four species are rare and poorly known. Three are found at depths of more than a thousand meters, but *P. arata* lives at the edge of the continental shelf at depths of 130 to 245 m. A new record for *P. arata* now increases the range for this species about 2100 km to the south off Miami. This range extension is surprising since the previously known range occupies a small area south of Cape Cod.

PHOTORECEPTORS OF THE BIVALVE *LYONSIA HYALINA:* THE EYES HAVE IT! Robert S. Prezant, Department of Biological Sciences, University of Southern Mississippi, Hattiesburg.

The siphons of the marine bivalve *Lyonsia hyalina* Conrad are often the only portion of the animal exposed to the outside world. As such they are well endowed with sensitive tentacles for tactile reception and also numerous small photoreptors densely packed along a band on the exhalent siphon. These "eyes" are composed of large, single celled vitreous lenses that are individually capped by an apical dome-shaped nucleus. The lenses, directed into the siphonal lumen, taper into a pigmented receptor portion that in turn is bound by five melanic pigment cells. The photoreceptors show common microstructural features of light gathering organs (i.e. numerous mitochondria, high glycogen concentrations) that includes an expanded photon-receptor region composed of elaborate cell membranes. In many protostomes this receptor region is typically composed of expanded microvillar membranes (i.e. rhabdomeric) but in *L. hyalina* the receptor is composed of whirls of ciliary membranes that form concentric rings in the proximal region of the tapered receptor zone. These flared, concentric membranes are unusual and found only in very few organisms. The ciliary basis of this bivalve's eyes may offer insight into their evolutionary status. *Laternula truncata* (Lamarck), another pandoracean bivalve, also possesses similar receptor structures (Adal and Morton, 1973; *J. Zool., Lond.* 171: 533–556). This common feature, in eyes that otherwise have different macrostructures, may reveal a lineage that is closer than previously suggested.

NEW FAMILIES OF ARCHAEOGASTROPOD LIMPETS IN THE HYDROTHERMAL VENT COMMUNITY. James H. McLean, Los Angeles County Museum of Natural History, California.

Four new limpet families (three of which have two or more species), are variously represented from seven, widely scattered, deep sea sites having the hydrothermal vent community. Gill, radular, and kidney characters are those of archaeogastropods but the families can not even be assigned to living superfamilies. Of these, only the Neomphalidae, represented by *Neomphalus fretterae* McLean, 1981, has yet been described; anatomy has been detailed by Fretter, Graham, and McLean (1981). Fretter and McLean are collaborating on the descriptions of the remaining three families. Each new family differs from the others and from the Trochacea at the superfamily level, which implies that all have common ancestry with trochaceans. It further suggests that the ancestors of the hydrothermal vent limpets, whether limpets or coiled gastropods, entered this community by the early Mesozoic, the time of origin of other living archaeogastropod superfamilies, a time at which archaeogastropods were the dominant gastropods in shallow seas. Basic anatomical and radular characters of the hydrothermal vent limpets are considered to be those of unrecognized archaeogastropod clades that otherwise suffered extinction in the late Paleozoic or early Mesozoic.

DISTRIBUTION PATTERNS OF FRESHWATER MUSSELS AT NORTH HOLSTON FORD, NORTH FORK HOLSTON RIVER, VIRGINIA. Helen E. Kitchel, Virginia Cooperative Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg.

During 1981 and 1982, 16 species of freshwater mussels were collected at North Holston Ford, North Fork Holston River. A mean density of 10.6 mussels/m^2 was estimated from sixty random 0.5m^2 quadrat samples, indicating a population of roughly 31,000 adult mussels for the study area. Quadrat samples contained 10 mussel species: *Actinonaias pectorosa, Fusconaia edgariana, Lampsilis fasciola, Lexingtonia dolabelloides, Medionidus conradicus, Pleurobema oviforme, Ptychobranchus fasciolaris, P. subtentum, Villosa nebulosa, V. vanuxemi.* Six additional species were collected in muskrat middens or by handpicking: *Alasmidonta marginata, A. minor, Fusconaia barnesiana, Lampsilis ovata, Lasmigona costata, Toxolasma lividus.* Mussel densities varied according to location at the site. Water depth, current velocity, and substrate composition followed a consistent longitudinal zonation throughout the study area. Shallow water and low velocity were associated with the left ascending bank, whereas deep water and high velocity were associated with the right ascending bank. Substrate samples exhibited similar zonation patterns, and increased in particle size from left to right ascending bank. The distribution of mussels appeared to be most closely correlated with substrate composition, and high species densities were associated with mixed sand, gravel, and pebble substrates. Habitat of the endangered *F. edgariana* was associated with areas of high mussel density and diversity, along the left ascending bank and around seasonally vegetated areas.

FRESHWATER MOLLUSCAN SURVEY OF THE ROANOKE, TAR AND NEUSE RIVER SYSTEMS, N.C. Arthur H. Clarke, Ecosearch, Inc. Mattapoisett, Massachusetts.

Systematic surveys of freshwater mollusks in northeastern North Carolina, sponsored by the Smithsonian Institution and the U.S. Department of the Interior, Fish and Wildlife Service, were carried out from 1977 to 1983. The Tar River System received special attention (72 study sites) because it contains *Elliptio* (*Canthyria*) *steinstansana* Johnson

& Clarke, a rare spiny mussel proposed for inclusion on the federal List of Endangered Species. Supplementary studies were also done in the lower Roanoke River System (13 sites) and the lower Neuse River System (14 sites) to assess the possibility of occurrence of *E. steinstansana* there.

The Tar River System is highly productive and, except for a reach below Rocky Mount, has good water quality. We found 26 species there of which 14 are Unionidae. The whole bivalve fauna is being impacted by *Corbicula fluminea* which was introduced there in 1979 or 1980. By the summer of 1982 it was dominant (ca, 1000/M^2) below Old Sparta and had reached N.C. Hwy. 44 north of Tarboro. By the summer of 1983 it had ascended an additional 40 miles to near Spring Hope and it will soon be conspicuous throughout the system.

The Roanoke River below Lake Gaston is heavily silted. It revealed only fresh empty shells of *Anodonta implicata* and *Elliptio complanata* and abundant *Corbicula*. In a river-lake of the Cashie River (a Roanoke tributary), we found empty shells of *Anodonta implicata* and *Lampsilis ochracea*, huge specimens of *Ligumia nasuta*, and no *Corbicula*. The Neuse River between Raleigh and Seven Springs yielded only *Elliptio complanata*, a rare unionid of unknown identity, and *Corbicula*. Among Neuse tributaries, the Trent River is polluted below Trenton and apparently has no mollusks there, but the Little River is productive and supports a diverse fauna.

RECENT NAIAD MOLLUSCS OF THE DETROIT RIVER.

Thomas M. Freitag, U.S. Army Corps of Engineers, Detroit District.

Although not a planned survey, qualitative mussel shell collections were made at two shore sites on the Detroit River: a dredge site near the mouth in Gibraltar, Michigan, in 1982, and from near the head of the river on Belle Isle, Detroit Michigan, in 1983 and 1984. Dredge site shells, although often appearing recent, are probably from long-dead individuals. Shells from Belle Isle were from muskrat middens and most had vestiges of flesh. Some live individuals were found. Juveniles of several species suggest that reproduction is taking place. Species composition was similar at both sites. A total of 29 recent species were found at Belle Isle. Michigan endangered species were: *Dysnomia torulosa rangiana, Simpsoniconcha ambigua,* and *Villosa fabalis*. Threatened species were: *Dysnomia triquetra* and *Obovaria subrotunda*. Detroit River museum specimens of species not found in this survey were: *Alasmidonta marginata, Alasmidonta viridis, Lampsilis fasciola* and *Quadrula quadrula*. Literature records of *Anodonta imbecillis, Lasmigona compressa* and *Quadrula pustulosa* are probably accurate since these species are found in adjacent waters. However, the literature record of *Fusconaia subrotunda* is probably in error and the record of *Leptodea leptodon* is doubtful. The presence of the Federally endangered species, *Dysnomia sulcata delicata*, in the Detroit River is doubtful, since the identity of museum specimens is uncertain and no recent specimens have been found. The original fauna of the Detroit River consisted of about 36 species.

Additional Species Found

Actinonaias carinata
Amblema plicata
Anodonta grandis grandis
Anodontoides ferussacianus
Carunculina parva
Cyclonaias tuberculata
Elliptio dilatata
Fusconaia flava
Lampsilis radiata siliquoidea
Lampsilis ventricosa
Lasmigona complanata
Lasmigona costata
Leptodea fragilis
Ligumia nasuta
Ligumia recta
Obliquaria reflexa
Obovaria olivaria
Pleurobema coccineum
Proptera alata
Ptychobranchus fasciolare
Strophitus undulatus
Truncilla donaciformis
Truncilla truncata
Villosa iris

AN EXAMINATION OF SOME C.S. RAFINESQUE NORTH AMERICAN UNIONID TAXA (BIVALVIA: UNIONIDAE).

Arthur E. Bogan, Department of Malacology, Academy of Natural Sciences of Philadelphia, Pennsylvania, **Lynn B. Starnes,** Tennessee Valley Authority, Knoxville and **James D. Williams,** Office of Endangered Species, U.S. Fish and Wildlife Service, Washington, DC.

The work of Samuel C. Rafinesque during the early half of the 19th century in natural history has long been a source of confusion and aggravation. His work examined here is restricted to those papers which discuss freshwater bivalves (1818–1832). Rafinesque's publications follow close upon the heels of Lamarck and Say's work on North American unionids and are contemporary with the works of Barnes, Conrad, Hildreth and the early work of Isaac Lea. Major problems with Rafinesque's freshwater bivalve work have been claimed by numerous authors. These problems include: lack of type materials or the deposition of materials in collections where the specimens could be examined, poor and inadequate descriptions, inadequate or no illustrations, and publication in obscure or inaccessible journals. A point of major concern at the time was Rafinesque's excessive splitting of what were then considered good species or genera. A major factor in the rejection of Rafinesque's unionid work was Isaac Lea's publication of a list of 108 Rafinesquean specific names as unidentifiable, while recognizing only 16 Rafinesquean specific names in his four synopses of the Unionidae (1836–1870). This attitude was further entrenched by the observations of Amos Binney about the sad state of Rafinesque's mental health. The rejection of Rafinesque's names and the general belief that most of his taxa were unrecognizable from their descriptions led C. T. Simpson to treat most Rafinesquean names as *nomina dubia*. Interestingly, Simpson missed some 20 species names coined by Rafinesque. This trend continues today. A complete tabulation and thorough examination of all the generic, specific, and varietal names has never been presented. We present a tabulation of his generic, specific and varietal level taxa. The list includes 34 generic and subgeneric names, 124 specific names and 55 varietal names. We specifically consider Rafinesque's species which have known extant types (61 species). The final picture which emerges of the work of Rafinesque is not that of a sick, deranged crackpot, but a dedicated eccentric naturalist with insufficient patience or funds, who was many years ahead of his time. As Bryant Walker observed, many of Rafinesque's names will have to be accepted based on a close examination of the original work and extant shell materials; other Rafinesquean names will obviously fall into synonomy, while many others will remain as either *nomina nuda* or *nomia dubia*.

OCCURRENCE AND DISTRIBUTION OF JUVENILE FRESHWATER MUSSELS IN A THIRD-ORDER STREAM. James C. Widlak, Virginia Cooperative Fishery Research Unit, V.P.I. & S.U., Blacksburg.

Potential habitats of juvenile mussels were systematically sampled to document their location and abundance. Fifteen quadrat samples (573 cm^2) were collected from each of three habitat types (riffle, run, pool) and two microhabitats (behind rocks, along banks). The 75 substratum samples were sieved into 5 particle size classes, and substratum composition was determined as percentage of total dry weight. Each fraction was examined for juvenile mussels under a dissecting microscope.

A total of 66 juvenile mussels were found ranging from 0.8–25.1 mm in length; 51% were found behind rocks, 19% in riffles and runs, 9% in pool habitat, and 2% along stream banks. Young-of-year (age 0) mussels were most abundant behind rocks, and older juveniles (age I–III) occurred in habitats similar to those of adult populations. Juveniles had a clumped distribution, apparently surviving better in riffles and behind rocks than in other habitats. Population stability appears to be maintained by the large number of age classes rather than high juvenile recruitment each year.

VALIDATION OF ANNULUS FORMATION ON FRESHWATER MUSSEL SHELLS AND A COMPARISON OF TWO AGEING TECHNIQUES. Steven N. Moyer, Virginia Cooperative Fishery Research Unit, Virginia Polytechnic Institute and State University, Blacksburg.

Age composition and growth characteristics of freshwater mussel populations are determined almost exclusively from external growth checks (annuli) on shells. However, shell erosion, environmentally-induced checks, and the obscurity of growth checks near shell margins usually result in approximate ages for this faunal group, particularly among older specimens. An internal ageing method involving thin-sectioning of valves was used to achieve the following objectives: 1) validate the deposition of one annulus each year, and 2) compare the utility of the thin-sectioning technique to counts of external annuli on valves.

To validate annulus deposition, mussels of four species were collected, tagged or marked, measured, and returned to three streams in southwestern Virginia. Following a set time period (1 to 3 years), tagged mussels were recovered and their shells examined internally and externally for the occurrence of annuli. Annulus formation was documented on many specimens representing all four species. Slow growth (< 1 mm/yr) prevented annulus confirmation on the remainder of recovered specimens.

Comparison of the internal and external ageing techniques was completed using specimens of *Fusconaia edgariana* and *Pleurobema oviforme* aged by both methods. Counts of external growth checks on valves consistently underestimated ages of specimens when compared to ages obtained by thin-sectioning. The thin-sectioning technique was the most accurate for ageing freshwater mussels and should be used, particularly for older specimens.

EFFECTS OF CONTAMINANTS ON NAIAD MOLLUSKS (UNIONIDAE): A REVIEW. Marian E. Havlik, Malacological Consultants, La Crosse, Wisconsin and **Leif L. Marking**, National Fishery Research Laboratory, La Crosse, Wisconsin.

The literature contains numerous reports on uptake in shell, storage in tissues, and elimination of contaminants, but information on toxic effects of contaminants to naiad mollusks is limited. Contaminants appear to have destroyed naiad populations and entire beds in some instances directly by toxic effects or indirectly by eliminations of food organisms or host fish. Fry of fish infected with 20–35 naiad glochidia were more sensitive than uninfected fish when exposed to toluene, naphthalene, and crude oil. Manganese seems to be the element that is most readily taken up and stored in tissues; some reports indicate tissue concentrations of thousands of ppm and suggest that the element is important in metabolism. Zinc and cadmium also accumulate at high levels in tissues. Concentrations of contaminants that were toxic to naiad mollusks were 16 ppm of arsenic trioxide, 18.7 ppm of copper, 10 ppm of copper sulfate, 700 ppm of phenol, 11 ppm of potassium, 1000 ppm of Thimet or Satox, and 5 ppm of ammonia. In long-term exposures, concentrations of copper as low as 25 ppb were lethal to naiades. Although few specific impacts of contaminants on naiades are evident in the literature, circumstantial evidence leaves little doubt that contaminants are responsible for decreases in population density, range and diversity. Few long-term toxicity tests have been done to assess sublethal effects or effects on growth and reproduction. The assignment of individual stresses responsible for the disappearance of naiad mollusks in contaminated areas is difficult or impossible with existing information. Rarely have individual components been quantitatively and qualitatively correlated with the composition and size of the naiad fauna, especially for contaminants. More often than not, two or more factors work in combination to produce the total stress that adversely affects populations of naiad mollusks. The exotic, *Corbicula*, can live in some environments that are no longer inhabited by the Unionid species, and *Corbicula* seem to be more resistant than native species to stresses related to contaminants. Naiad mollusks are important indicators of contaminants in the environment, and residues in soft-tissue indicate recent or present contamination while residues in shell material indicate exposure to contaminants in the past.

JET PRESSURE AS AN INDEX OF METABOLIC RATE IN FREE-SWIMMING SQUID. D. M. Webber. and **R. K. O'Dor** Department of Biology, Dalhousie University, Halifax, Nova Scotia.

Squid swim by converting the pressure-volume (P-V) work produced by mantle muscle contractions into jet thrust. A pressure transducer measuring intra-mantle pressure via a cannula, allowed monitoring of total P-V work associated with swimming and respiration in squid (*Illex illecebrosus*) in a Brett-type tunnel respirometer. Squid were "calibrated" by simultaneously measuring pressure and oxygen consumption at various swimming speeds. Animals ranged in weight and length from 200–556g and 25–50cm. Oxygen consumption increased logarithmically with swimming speed. The maximum or critical velocity, as defined by Brett, a squid can swim is between 70 and 90 cm/s, approximately 2 body lengths/s. Burst swimming velocity from individual jets reached 1.8m/s. Values for oxygen consumption were the highest recorded for marine poikilotherms of this size; 348 ml/Kg/h for standard metabolism and 1245 ml/Kg/h for maximum velocity. The relation (r = 0.82) predicting oxygen consumption at various combinations of weight and velocity is:

$$\mathrm{OxCons} = 0.246 * \mathrm{Weight(g)}^{1.06} * 1.016^{\mathrm{Velocity}}$$

At 40 cm/s, a plausible migrating velocity, oxygen consumption is 660 ml/Kg/h. Total pressure generated increased linearly with oxygen consumption as a result of both increasing jet frequency and pressure. The oxygen-pressure relation is highly correlated over a wide range of velocities (r = .97). Burst jet pressure ranged from $4 * 10^4$ N/m^2 to $5 * 10^4$ N/m^2. A telemetering ultrasonic pressure transducer was tested in free-swimming squid measuring intra-mantle pressure. The high correlation of the oxygen-pressure relation means that such telemetry has great promise as a means of studying the activity and bioenergetics of cephalopods in nature.

INDEX TO SPECIES OF MOLLUSCA 1850–1870: SUPPLEMENT 1. Joseph Rosewater, Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC.

A supplement is being prepared to "Index to the Species of Mollusca Introduced from 1850–1870" by F. Ruhoff, 1980. To date colleagues have advised of some 50 works that must be reviewed for additional taxa. Three of these yielded several hundred new names: Emmons, E., 1858, "Descriptions of the Fossils of the Marl Beds," *In* Report of the North Carolina Survey Agriculture of the Eastern Counties; Dunker W., 1864, *In* Grube, A. E. "Die Insel Lussin und ihre Meeresfauna.": Mörch, O. A. L. 1852–1853. "Catalogus Conchyliorum . . . Comes de Yoldi." The latter offers special problems for recognition of names. Although listed by Ruhoff, it is difficult to discover any taxa she included from it. A large number of names were introduced by Mörch in association with plate references to the "Conchylien Cabinet" by Martini-Chemnitz (*Tryonia* 2:1–427, 1979). References received as omissions must be carefully searched for taxa. In a few cases, such as Adams, A. and Reeve, L., 1848–1850, "The Zoology of *H. M. S. Samarang*", the names already are included in Sherborns's "Index Animalium" and will not be repeated in the Supplement. It is advisable to check Sherborn's "Index" for species described near 1850 because they may be included. New taxa may not be recognized in works such as Mörch unless they are scrutinized carefully. Completion of Supplement 1 is a long term project. It will be appreciated if discoverers of omissions will continue to send references.

Microcomputer users may be interested to know that a "relational data base" program can be of considerable help in the preparation of works like the Supplement. Where repetitive data sets are being assembled, eg.: species name, genus, author, date, reference, it is possible to enter them in random order. Later, this information is sorted and arranged by the computer and the resulting listing is automatically converted to a word-processing program for final manuscript editing. The completed manuscript on a "floppy disc" may be sent directly to the printer for production of the publication.

HABITAT IMPROVEMENT AS A MANAGEMENT TOOL IN THE CONTROL OF EXOTIC MOLLUSCS. Marc Imlay, Columbia, Missouri.

Introduced molluscs from Africa, Europe, and Asia are a medical economic, and ecological liability in this country and around the world. There are three traditional strategies used in the war against exotic species: prevent entry, chemical control, and biological control. Preventing entry is difficult to enforce. Chemicals exert an undesirable to intolerable effect on other resources. Biological control organisms have become more serious pests in their own right. I believe that habitat improvement is also a valuable tool for control of exotic species. It appears the native fauna can survive either competition from exotics or moderate pollution (or moderate habitat degradation) but not both at the same time.

ANNUAL BUSINESS MEETING
REPORT FOR 1984

The 50th annual business meeting of the American Malacological Union was called to order by President Robert Robertston at 3:15 p.m. Friday, July 27, 1984 in the James and Elizabeth Room, Holiday Inn Hotel, Norfolk, Virginia. President Robertson announced registration was 180, including participants from 10 foreign countries.

Minutes of the 1983 meeting, as published in the *Bulletin*, were approved. Summaries of officer and committee reports were approved. Full accounts are filed with the Recording Secretary. Membership and subscription totalled 722 for 1983. The full financial report is printed below.

The Symposium Endowment Fund gained $2202.25 from this meeting's book auction. Donations received at this meeting assured the fund would be well over $16,000. (Total for the fund now determined to be $18,053.49).

Editor Robert Prezant reported that 1200 copies of Vol. 2 had been printed at the cost of $6783.13. Vol. 3 (1) is expected for delivery in early Fall, 1984. Vol. 3 (2) will be delivered in Spring, 1985 and will contain symposia of this meeting.

The following budget was adopted for 1985:

INCOME		
Memberships (all except life)		$11,000.00
Sales		
HTSCS		250.00
Rare & End		5.00
Bulletin back issues		300.00
Teskey Index		25.00
	SUBTOTAL SALES:	(580.00)
Bulletin Receipts (Page Chgs., Reprints)		2,000.00
Proceeds of Meeting		500.00
Donations, Symposium of that year		500.00
Miscellaneous		100.00
Interest on Symposium Endowment Fund		1,200.00
	TOTAL:	$15,880.00
Interest-General Savings (not added to income)		580.00
DISBURSEMENTS		
Bulletin (Inc. life interest)		$ 9,000.00
Newsletter		900.00
Membership Committee		125.00
President's Organizing Fund		500.00
Officers to meeting (2 Sectrys., Treas., Editor)		2,000.00
Postage (minus *Bulletin* and Newsletter)		700.00
Printing (minus *Bulletin* and Newsletter)		300.00
Office Supplies		100.00
Postal Permit		45.00
Miscellaneous		300.00
Annual Meeting Expense		150.00
Ads (Meetings, HTSCS, etc.)		250.00
Symposium Subsidy		500.00
Symposium Expenses (Endowment interest)		1,200.00
Student Prize		250.00
	TOTAL:	$16,320.00
SUMMARY		
Income		$15,880.00
Disbursements		16,320.00
Interest-general		580.00
Net gain		140.00

A Resolution from the Conservation Committee via Council was adopted as follows: "Resolved that the President of AMU should send a letter to the Director of the US Fish and Wildlife Service petitioning that *Io fluvialis* be considered for endangered or threatened status with appropriate critical habitat designated."

This committee reported that a list of invertebrate species suggested for potential listing as endangered or threatened has been published by the US Fish and Wildlife Service and that many mollusks were included.

It was announced that the 35 acre Pendleton Island complex on the Clinch River has been purchased by The Nature Conservancy. The Tar River spiny mussel listing package has been completed, and this species appears likely to be listed as endangered.

Dr. Melbourne Carriker, incoming president, announced plans for symposia on molluscan radulae and molluscan capsules at the 1985 meeting to be held July 29–August 3 at the University of Rhode Island at Kingston. There will be a symposium on freshwater mollusks also, workshops, and field trips. An auction to benefit the Symposium Endowment Fund will be held. The Boston Malacological Club, celebrating its 75th anniversary in 1985, will have a commemoration party. A program to honor junior malacologists will open the session. Three prices of dormitory rooms should aid attendance. Plans approved.

Motion approved as follows: "The site for the 1986 annual meeting of the American Malacological Union will be Monterey, California."

Approved by acclamation, the following slate of officers, due to be elected at this meeting, was voted:

President:	Melbourne Carriker (one year)
President-Elect:	James Nybakken (one year)
Vice-President:	William Lyons (one year)
Treasurer	Anne Joffe (three years)
Editor	Robert Prezant (five years)
Councillors-At-Large	Roger Hanlon (two years)
	John B. Burch (two years)

The Committee on Revision of the Constitution and By-Laws, composed of Drs. Harold Murray, Alan Solem, and Joseph Rosewater, had brought for consideration a plan to restructure Council. No vote was recommended for 1984, but this plan was posted for all members to read and discuss. A motion was adopted authorizing the resubmission in 1985 of a plan to restructure Council. Another motion approved the publication of the plan in an AMU Newsletter before next year's meeting.

Motions adopted on revisions to the By-Laws follow:

1. Article I, section 3, part a
   "Regular Membership: $20.00 per year for an individual. Additional members of the Immediate Family, spouse, or children may become Regular Members for $1.00 per year each, but will not receive a separate set of publications. A bonafide student may become a Regular Member for a fee of $15.00 a year."
2. Article I, section 3, part b
   "Corresponding Membership: Current Regular Membership dues plus postage as set by the Publications Committee."
3. Article I, section 3, part f
   "Affiliated Membership: $22.00 for each shell club or similar organization."
4. Article III, section 2, part b
   "The President-Elect shall function as chief planner and coordinator of the annual meeting for which he/she is elected as President, and shall act for the current President if the latter is unable to serve."
5. Article III, section 2, part c
   "The Vice-President shall assist the President on request and shall serve as Chairman of the Annual Meeting Site Committee with the responsibility for arranging for and announcing the site of the Annual Meeting that will be held when the now Vice-President will be President of the AMU."
6. Article III, section 2, part d
   "The Corresponding Secretary shall handle all correspondence of general inquiry of the nature of AMU, shall assist the President in handling publicity of the Annual Meeting, shall handle correspondence of appreciation after each meeting, shall be Editor of the Newsletter, shall produce and mail the Newsletter seeking advice of the Publications Committee, if necessary; shall provide mailing lists of membership, shall handle the sale of all publications except the *American Malacological Bulletin* and its back issues, and shall report to Council annually on activities."
7. Article III, section 2, part e
   "The Recording Secretary shall record, distribute, and maintain the minutes of the Council and annual Business Meeting, shall maintain the official record of members and subscriptions, shall prepare the membership list for publication, shall inform new members of their acceptance, shall act as agent for sale of back issues of the *American Malacological Bulletin*, and shall report annually to the Council and the Annual Business Meeting."

A motion adopted on revision of the Constitution follows (subject to mail vote from all Regular Members): "Eliminate article V from the Constitution." This concerns geographical divisions. A favorable vote on this revision will change the numbering of the following Articles: VI to V, VII to VI, VIII to VII, IX to VIII.

The President announced new membership applications have been printed. He reported that the AMU Archives are in refurbished rooms at ANSP and that equipment has been purchased with the Jack Parker Memorial Funds to house the extensive and historically important Karl Jacobson correspondence.

The Council of Systematic Malacologists report was approved as follows:

1. The common names lists are nearing completion and first drafts were on display at this meeting. (Dr. Donna Turgeon, chairman of the common names committee, was given approval at this annual session to publish this working draft in *Shells and Sea Life*.)
2. CSM approved a letter to be sent supporting the request from the Australian Malacological Society to deposit Australian mollusk types in Australian public museums where ready access is available to those most involved with local studies.
3. CSM will establish a committee to provide a report to ASC in 1985 on the availability and needs of American malacology for a faunal survey of Mollusca of the U.S.A.

Walter Sage, chairman of the AMU exhibits committee this year, was commended by Council for his efforts to establish commercial and non-commercial exhibits at the annual meeting. He informed Council he would not be able to continue.

Commercial and non-commercial exhibits were approved by Council for the 1984 meeting by mail vote. Members approved the following motion to establish future policy on exhibits:

1. "Exhibits and Commercial sales of items of interest to AMU members shall be encouraged at annual meetings.
2. An Exhibits Manager shall be appointed by the President, initial term of 5 years (must be reappointed each year according to Constitution), whose authority over exhibits shall be total. The task of this manager may be augmented with help from the local committee.
3. Exhibits shall be in good taste as determined by the Exhibits Manager. Exhibitors will be expected to abide by 'Exhibits Rules and Regulations' made available to each. (An extensive list of such rules and regulations has been prepared by the initial committee and is on file).
4. Commercial exhibitors may be charged a fee the amount of which will be determined by Council. At the outset, a fee of $50.00 is suggested. Said fee may be waived for non-commercial or non-profit exhibitors.
5. For purposes of protecting both the AMU and potential exhibitors, it is recommended that general liability insurance be acquired in an amount sufficient to cover exhibits and also general activities at the annual meetings."

Another motion from Council called for appointment of a chairman of these exhibits but prohibited the sale of shells. The latter phrase was struck from this motion. Adopted as follows: "The next president will appoint a person to act as chairman of commercial and non-commercial exhibits."

In addition to the exhibits of commercial and noncommerical shells, Dr. Carriker expressed the desire to include shells and related items in the 1985 AMU auction. The precedent for this was established with a motion in 1980 to approve sale of such items at the Fort Lauderdale annual meeting, with all funds to go to AMU. Funds from the 1985 auction will go to the Symposium Endowment Fund.

It was announced that Biology 83/84, which AMU had voted to provide information for, is defunct.

The President announced that AMU will share in the disposition of property of the late Maude W. Meyer, a longtime AMU member.

A motion was approved that $150.00 be authorized for a second student award at this meeting, utilizing donations from members in 1983 for this purpose.

The following motion concerning membership was approved: "Membership responsibilities will be vested in the Finance Committee, with the same members serving for several years in order to achieve some degree of continuity in the approach to the membership problem."

The motion to reduce the price of the Index to the Bulletins, 1934–1974, to $2.00, including postage in the U.S., was approved.

Motions were unanimously approved to give a vote of thanks to Myra Taylor for her many years as Treasurer of AMU and to thank Dorothy Beetle for serving as Newsletter Editor for many years.

A motion was approved commending the 1984 Constitution and By-Laws Committee for the presentation of plans to change the structure of Council.

A motion was approved commending Dr. Robert Robertson for this fine annual meeting.

A motion was approved to send greetings to those honorary life members not present.

Meeting adjourned at 5 p.m.

Constance E. Boone, Recording Secretary

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1983

CHECK BOOK BALANCE, JANUARY 1, 1983			$ 4,249.06
RECEIPTS:			
Memberships:			
Regular	$ 9,260.00		
Life	556.50		
Sustaining	120.00		
Corresponding	487.00		
Clubs	1,054.50		
Institutions	697.00		
	12,175.00	12,175.00	
Sales:			
Rare & Endangered Species	60.58		
How To Study & Collect Shells	214.25		
Teskey Index	-0-		
Back Issues, Old *Bulletins*	150.00		
New *Bulletin*	28.00		
	452.83	452.83	
Other Receipts:			
1982 Page Charges, Paid in 1983	78.75		
New Bulletin Money (From R. Prezant)	743.82		
Allen Press Check (BIOLOGY 83-Kohn)	500.00		
Best Student Paper	146.50		
Publish Student Papers	274.50		
Endowment Fund Donations	4,242.00		
Previous Symposium Participants' Returned to Endowment Fund	500.00		
Seattle Auction for Endowment Fund	1,182.00		
Interest From Endowment Withdrawn For Seattle Expenditures	875.06		
Seattle Registration Monies (Kohn)	2,050.00		
Life Membership Interest (5/83)	899.31		
Re-deposit of No Signature Checks	42.00		
SASA Savings Withdrawal	3,663.72		
Miscellaneous	32.38		
	15,230.14	$ 15,230.14	
Total Cash Receipts Acounted For	27,857.97		
TOTAL CASH ACCOUNTED FOR:		$32,107.03	
DISBURSEMENTS:			
AMU BULLETIN, INCL. POSTAGE, PRINTING, ETC.	$ 9,628.65		
AMU NEWSLETTERS, INCL. POSTAGE, PRINTING, ETC.	1,384.56		
Other Postage	623.43		
Other Printing	259.10		
Office Supplies	187.92		
Bequaert Memorial Student Award	400.00		

Dues and Advertising	252.50
New Petty Cash Account—Corresponding Secretary	75.00
Parker Memorial Funds to Archives	442.00
New Calculator For Treasurer	79.97
Allen Press Funds To ANSP (Kohn)	500.00
California Filing Fees	7.50
Officers' Travel	2,187.83
Refund	45.03
Checks Returned For Signature (2)	42.00
Miscellaneous	39.23
Refunds To Seattle Registrants	1,566.00
Bus For Seattle Meeting	495.00
Musicians For Seattle Meeting	300.00
Symposium Expenses—Seattle	2,788.22
Student Award—Seattle	250.00
	21,553.94
Endowment Fund Monies Deposited in Long Term Term Certificates	7,917.40
Total Disbursements from All Activities	29,471.34

CHECK BOOK BALANCE, JANUARY 1, 1983	$ 4,249.06
TOTAL RECEIPTS	27,857.97
TOTAL CASH	32,107.03
TOTAL DISBURSEMENTS	29,471.34
CHECK BOOK BALANCE, DECEMBER 31, 1983	2,635.69

RECAPITULATION OF ASSETS, DECEMBER 31, 1983:

Cash in Checking Acct., Mercantile Bank		$ 2,635.69	
Editor's Fund		1,522.39	
Treasurer's Petty Cash		20.00	
Recording Secretary's Petty Cash		300.00	
Corresponding Secretary's Petty Cash		75.00	
SASA Acct. #22-906859		2,923.20	
1st Federal Money Market Endowment Fund Acct. #6300834-02		5,257.36	
1st Federal Certificate of Deposit Endowment Fund Acct. #6800057.02		2, 684.38	
Bexar Savings Money Market Endowment Fund Acct. #501-900-03		5,414.68	
TOTAL ASSETS		$20,832.70	
LIFE MEMBERSHIP ACCT. #5-906860	$ 3,525.25		
AMU NET WORTH, DECEMBER 31, 1983			$20.832.70
CHANGES IN CAPITAL ACCOUNT:			
AMU Capital Account, January 1, 1983			16,262.42
AMU Capital Account, December 31, 1983			20,832.70
NET INCREASE IN ASSETS, 1983			$ 4,570.28

Respectfully Submitted,
MYRA L. TAYLOR, TREASURER

AMERICAN MALACOLOGICAL UNION, INC.
EXECUTIVE COUNCIL
1984–1985

OFFICERS

President	Melbourne R. Carriker
President Elect	James Nybakken
Vice-President	William G. Lyons
Treasurer	Anne Joffe
Recording Secretary	Constance E. Boone
Bulletin Editor	Robert S. Prezant
Corresponding Secretary (Newsletter Editor)	Paula Mikkelsen
Councillors-At-Large	Paul Mikkelsen, Barry Roth Roger Hanlon, John B. Burch

COUNCIL
PAST PRESIDENTS
(Current Members)

Harald A. Rehder (1941)
Henry van der Schalie (1946–47)
A. Myra Keen (1948)
A. Byron Leonard (1953)
Ruth D. Turner (1957)
R. Tucker Abbott (1959)
Thomas E. Pulley (1961)
William K. Emerson (1962)
Albert R. Mead (1963)
Juan J. Parodiz (1965)
Ralph W. Dexter (1966)
Arthur H. Clarke (1968)
Joseph Rosewater (1969)
Alan Solem (1970)
David H. Stansbery (1971)
Arthur S. Merrill (1972)
Dee S. Dundee (1973)
Harold D. Murray (1974)
Donald R. Moore (1975)
Dorothea S. Franzen (1976)
George M. Davis (1977)
Carol B. Stein (1978)
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(Revised September 1, 1984)

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ANDERS, KIRK W., Shells of the Seas, Inc., P.O. Box 1418, Ft. Lauderdale, FL 33302 (Volutidae; all rare shells).

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ATKINSON, DR. JAMES W., and ELIZABETH H., Dept. of Naural Science, Michigan State University, East Lansing, MI 48824 (Developmental biology; Terrestrial pulmonates—special emphasis on pattern formation in relation to spiral cleavage and gametogenesis—also evolutionary mechanisms which emerge from developmental events).

AUFFENBERG, KURT, Museum Technician, Florida State Museum, Univ. of Florida, Museum Rd., Gainesville, FL 32611 (Neritacea: Neritidae).

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BELANGER, SCOTT E., Univ. Center for Environmental Studies, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA 24061 (*Corbicula* ecology, industrial biofouling by *Corbicula*, aquatic ecotoricology).

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BLEAKNEY, DR. J. SHERMAN, Dept of Biology, Acadia Univ., Wolfville, Nova Scotia, Canada BOP 1XO (Nudibranchs, sacoglossans; ecology, zoogeography, systematics).

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BLOOM, JONATHAN A., RR6, Box 122, Town & Country TR CT., Carbondale, Il 62901 (Temporal changes in species diversity of freshwater mussels in Eastern U.S.).

BLUM, BERNARD J., 67–11 Beach Channel Drive, Arverne, Queens, NY 11692 (*Donax*).

BŌDY, RALPH L., 2538 10th Ave. W., Seattle, WA 98119 (Taxonomy).

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CALDWELL, DR. RONALD S., Science Program, Arkansas College, Batesville, AR 72501 (Arkansas land snails, nutrient cycling in land snails).

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CLARKE, DR. ARTHUR H., Ecosearch, Inc., 7 Hawthorn St., Mattapoisett, MA 02739.

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COOVERT, GARY A., 36 Prospect Ave., Dayton, OH 45415 (Taxonomy of worldwide mollusca; esp. Pectinidae).

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CORGAN, DR. JAMES X., Dept. of Geology, Austin Peay State Univ., Clarksville, TN 37040 (Pyramidellidae, Vitrinellidae, scaphopods, Tertiary faunas.

COSMAN, DIETER, 3051 State Road 84, Ft. Lauderdale, FL 33312 (Marine tropical and subtropical Gastropoda and Bivalvia worldwide).

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EVERSOLE, DR. ARNOLD G., Assistant Prof., Dept. of Entomology, Fisheries and Wildlife, Clemson Univ., Clemson, SC 29631 (Interpopulation variation and bioenergetics of molluscan populations).

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GARVIE, CHRISTOPHER L., 293 Liberty St., Long Branch, NJ 07740 (US Gulf Coast early Tertiary molluscs).

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GRUBER, GREGORY L., College of Marine Studies, University of Delaware, Lewes, DE 19958 (Reproduction, physiology, chemoreception, behavior of marine mollusks, environmental pollution).

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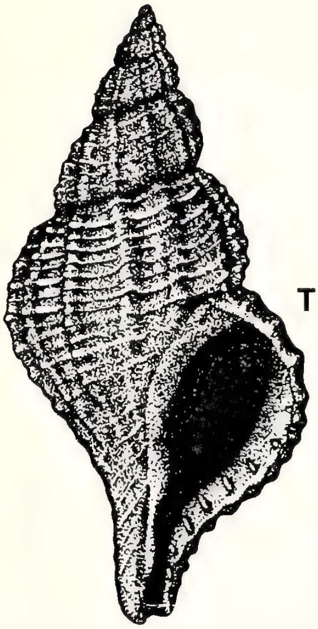

51st ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
UNIVERSITY OF RHODE ISLAND
JULY 29–AUGUST 3, 1985

The 1985 American Malacological Meeting will be held at the beautiful University of Rhode Island Campus in Kingston. The University offers a variety of inexpensive dormitory facilities or, for those preferring other arrangements, a Holiday Inn is four miles from Campus and other motels are 6 to 10 miles away. Kingston can be reached by Amtrak from Boston and New York; other travel possibilities include flights to Boston and a bus to Kingston (65 miles from Boston to Kingston), or flights to Providence (22 miles from Kingston) and special arrangements to Kingston.

The Boston Malacological Club is planning special events in commemoration of its 75th anniversary. There will be contributed papers, a poster session, marine and freshwater field trips, workshops, an auction to benefit the Symposium Endowment Fund, exhibits and commercial sales of items of interest to AMU members, and a New England clam bake. A program to honor junior malacologists will open the session.

Three symposia are also planned:

BIOLOGY OF MOLLUSCAN EGG CAPSULES
(Organized by Jan Pechenik)

BIOLOGY OF MOLLUSCAN RADULAE
(Organized by Robert Bullock and Carole Hickman)

ECOLOGY OF FRESHWATER MOLLUSCS
(Organized by Eileen Jokinen)

The Kingston area is a popular vacation spot with many interesting historical and geographical areas awaiting AMU visitors to New England. Beaches are only 6 miles from the Campus, Newport is 17 miles across the bay, and Mystic Sea Port is just across the state line in Connecticut. Make plans now to attend the 1985 AMU meeting in Rhode Island.

For further information please contact:
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Lewes, Delaware 19958 U.S.A.

MOLLUSCA: COMMON NAMES

A preliminary list of scientific and vernacular names of mollusks has been prepared by a committee from the Council of Systematic Malacologists (CSM), American Malacological Union (AMU). The list is intended to cover those species occurring on the American continent north of Mexico and/or generally within 200 miles of its margin (to 200 m), including coastal islands, but not the West Indies. Principles governing the selection of common names were developed by the Names of Invertebrates Committee of the American Fisheries Society (AFS). This committee's main goal is to achieve uniformity and avoid confusion in vernacular nomenclature of aquatic invertebrates.

In 1983, CSM adopted the AFS principles and elected to join that Society's effort to establish common names for aquatic invertebrates. CSM's list covers living terrestrial, freshwater, and marine mollusks that have been prevously described and published, preferably in monographed systematic works. Common names have been provided for most, but not all species. AFS intends to publish the mollusk list developed by AMU within the next five years, and to publish a revision every ten years. The AFS list as it is developed and published will also include crustaceans, other groups of aquatic invertebrates, and probably terrestrial mollusks to show AFS's appreciation of CSM's and AMU's cooperative efforts.

Within the next few months, the governing principles and the draft preliminary list for terrestrial mollusks is scheduled to appear in the monthly publication *Shells and Sea Life* (505 E. Pasadena, Phoenix, AZ 85012); freshwater and marine mollusk lists will follow. The draft lists are bring presented to an expanded shell audience for further review and comment. Selected comments will be published, thereby providing a forum for discussion. All draft lists of molluscan groups should be published before next year's AMU meeting.

Any questions on this CSM project should be directed to the committee chairman Dr. Donna D. Turgeon, Regulations Branch Chief, F/M12, National Marine Fisheries Service, Page Bldg. II, 3300 Whitehaven Street N.W., Washington, D.C. 20235; phone 202-634-7432.

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CONTRIBUTOR INFORMATION

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VOLUME 3, NUMBER 2 JUNE 1985

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Cover. *Io fluvialis* (Say), the logo of the American Malacological Union, represents the largest of the North American Pleuroceridae.

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June 1985

INTERNATIONAL SYMPOSIUM ON THE PHYSIOLOGICAL ECOLOGY OF FRESHWATER MOLLUSCS HONORING DR. W. D. RUSSELL-HUNTER

ORGANIZED BY
ALBERT J. BURKY, UNIVERSITY OF DAYTON
AND
ROBERT F. McMAHON, UNIVERSITY OF TEXAS AT ARLINGTON

AMERICAN MALACOLOGICAL UNION
NORFOLK, VIRGINIA July 1984

PHYSIOLOGICAL ECOLOGY OF FRESHWATER MOLLUSCS: CONTRIBUTIONS OF W. D. RUSSELL-HUNTER

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The symposium on *The Physiological Ecology of Freshwater Molluscs Honoring Dr. W. D. Russell-Hunter* and the publication of its proceedings in this volume of the *American Malacological Bulletin* have taken place at a particularly auspicious time. Certainly, as the entire field of physiological ecology seems to be undergoing a renaissance, it has given the symposium participants the opportunity to review and discuss both old, widely accepted concepts, and new approaches and hypotheses in physiological ecology, not only as they apply directly to studies of freshwater molluscs, but also, to the field as a whole. Indeed, one of us (RFM) recently participated in a symposium on Physiological Ecology, organized by Dr. Peter Calow at the 1984 meetings of the Society for Experimental Zoology, in Glasgow, Scotland (10–11 July, 1984), at which it became obvious that both theoretical bioenergetics, optimalization theory and bioenergetic analyses of life history tactics were becoming important new topics of study, at the same time that older concepts such as adaptation, environmental stress, and physiological acclimation or compensation were being questioned and opened to radically new interpretations. The reader of these symposium papers will find that many of these same questions are being approached by researchers investigating a wide variety of aspects of the physiological ecology of freshwater molluscs. Indeed, the published symposium papers in this volume represent a range of research interests that are nearly as broad as the entire subject area of physiological ecology. Thus, within this symposium proceedings appear papers describing a wide variety of research problems that fall on the broad continuum of research interests that span ecology and physiology. Some of the papers are concerned with more ecologically oriented topics, such as those by Kenneth Brown and Daniel Buckley on the genetic and physiological bases of life history adaptations. Others fall more squarely within physiological ecology, such as those of David Aldridge, Daniel Hornbach, and Bruno Streit on bioenergetic partitioning in relation to reproductive tactics and life cycles; of W. D. Russell-Hunter on tissue degrowth; of Jay Tashiro on the relative contributions of filter feeding and grazing in *Bithynia*; and of Albert Burky, Robert McMahon and Carol Williams on seasonal compensation in filtration and oxygen consumption rates. Other papers are more physiologically oriented, such as those of Thomas Dietz on ionic regulation and of Colin Little on renal adaptations. It was the authors' intention in organizing this symposium to include speakers with a wide variety of research interests within the physiological ecology of freshwater molluscs, both as a reflection of the considerable pedagogical and scholarly accomplishments of the man it honors and to provide a forum that would stimulate the exchange and, perhaps, initiate an eventual synthesis of new concepts, hypotheses and experimental approaches from the broad range of disciplines represented by the symposium participants.

The study of animal physiological ecology has its origins in the comparative physiology of intertidal, estuarine and marine organisms. The extreme variation of environmental conditions in these environments attracted investigators interested in elucidating the adaptations that allowed species to survive and proliferate under what appeared to be highly unstable and physiologically stressful habitats. Certainly, this tradition continues as the majority of research on the physiological ecology of invertebrate animals is still being focused on intertidal, estuarine and marine species (for reviews of the physiological ecology of marine invertebrates see Vernberg and Vernberg, 1972; Newell, 1976, 1979).

It appears to be the unspoken opinion of many researchers that freshwater species are not as interesting subjects for the study of physiological ecology as are marine species because their freshwater habitats are generally much more stable than are marine environments. As such, it is suggested that freshwater habitats cannot provide the levels of environmental variation required to allow comparative studies of freshwater species to reveal evolutionary relationships in their physiological, bioenergetic and life history adaptations.

It should become obvious to the reader of these symposium proceedings that such prejudicial assumptions about freshwater habitats are not based in fact. Most physiological ecologists investigating freshwater species would be quick to point out that freshwater habitats can be as variable and unstable as their marine counterparts. For example, marine intertidal habitats are described as highly variable in temperature as a result of the tidal cycle (Newell, 1979). However, freshwater habitats can have equally unstable temperature regimes. Those of freshwater molluscs have been reported to vary diurnally by up to 15°C (Boycott, 1936; Russell Hunter, 1953a; Appleton, 1976; McMahon, 1983). Another example involves adaptation to exposure in air. Animals in estuarine and intertidal habitats are periodically exposed to air and subsequent desiccation stress by receding tides. While such exposures are rarely for more than a few hours, some species living in the highest levels of the littoral zone can be emerged for periods of 8 to 10 days before being flooded by spring tides (McMahon and Russell-Hunter, 1977, 1981; Newell, 1979). In contrast, sedentary freshwater species may be exposed to air for weeks, months or even up to a year when their freshwater habitats recede or totally disappear during droughts or dry seasons. Under such conditions, freshwater species, including molluscs, must have adaptations that allow them to be much more tolerant of desiccation than are marine intertidal species. Indeed, many freshwater molluscs have been reported to be highly tolerant of dessiccation stress (Rang, 1834; Cheatum, 1934; Olivier, 1956; Olivier and Barbosa, 1956; von Brand, 1957; Dance, 1958; Clampitt, 1970; Newman and Thomas, 1975; McMahon, 1979; White, 1979) and to have evolved much more sophisticated adaptations to emersion than marine intertidal species (von Brand, et al., 1957; Collins, 1957; Burky, et al., 1972, 1985; Collins, 1957; Dietz, 1974; Newman and Thomas, 1975; McMahon, 1979; McMahon and Williams, 1984).

As these two examples indicate (and there are many others), freshwater animals, as do their marine counterparts, represent exceptional systems for the study of environmental adaptation. Certainly, it is only the intensive study of the physiological ecology of both marine and freshwater organisms that will eventually allow an understanding of the complex evolutionary pathways that have led from marine to freshwater species in a truly comparative sense. These symposium proceedings show that investigators of the physiological ecology of freshwater molluscs have made important new advances on a broad research horizon extending from the bioenergetic analysis of life history strategies to the comparative study of physiological plasticity and adaptation. It is our hope that this symposium will not only describe these new advances, but will also stimulate the interest of other investigators in the physiological ecology of freshwater invertebrates, especially that of the molluscs, which make excellent model systems for such studies.

Dr. W. D. Russell-Hunter, the research scientist in whose honor this symposium on the Physiological Ecology of Freshwater Molluscs was organized, has always understood the advantages of working with both marine and freshwater systems. He has published the results of research on both freshwater and marine molluscs throughout a research career spanning nearly 40 years. Although this symposium was limited to freshwater molluscs for the purpose of continuity and to meet size limitations, Dr. Russell-Hunter is equally recognized for his studies of marine molluscs as he is for his research on freshwater species. Indeed, it is his broad research background with molluscs, reflected in these symposium proceedings, which has made him uniquely able, in a field characterized by increasingly more narrowly defined research specialities, to formulate syntheses of major research problems overlapping several disciplines (Russell-Hunter, 1983a; Russell-Hunter and Buckley, 1983).

Dr. Russell-Hunter completed both his undergraduate and graduate studies at The University of Glasgow, Scotland. He took a position as an Assistant Lecturer at The University of Glasgow in 1948 while still continuing his graduate research under the direction of the noted experimental malacologist C. M. Yonge, who is famous for studies of the functional morphology of marine molluscs and is dean of European malacologists. He was promoted to University Lecturer in 1951 and was awarded a Ph.D. degree from The University of Glasgow in 1953. He was further honored by The University of Glasgow with the conferral of a Doctor of Science Degree in 1961 as an acknowledgement of his research achievements. He first began visiting the United States as an independent summer investigator and lecturer in the Invertebrate Zoology Course at the Marine Biological Laboratory in 1961. Fortunately for his American students, he moved permanently to the United States in 1963, when he accepted the position of Professor in the Department of Zoology (now Biology) of Syracuse University, where he remains today.

Surprisingly, Dr. Russell-Hunter's earliest research interests were not in the area of malacology. Rather, during World War II he was involved with a marine anti-fouling research program as a Scientific Officer with a B.I.S.R.A./British Admiralty team. Accordingly, his first published papers were on the settlement of marine diatoms (Russell Hunter, 1948) and heavy metal poisoning (Russell Hunter, 1949a). During the war, as part of his honors research at The University of Glasgow, he also began to focus on marine molluscs. This research led to the publication of classic works on the functional morphology and behavior of marine boring bivalves of the genus, *Hiatella* (Russell Hunter, 1949b, 1951).

By 1948 Dr. Russell-Hunter turned from the study of marine organisms to that of freshwater species, particularly the gastropods, a group that had previously received very little serious experimental attention. This shift in interest may have been partially a result of his appointment at that time as a lecturer in freshwater biology at The University of Glasgow. During this period he began to carry out experiments on freshwater molluscs at The University's field station at Rossdhu on the shores of Loch Lomond. In 1952 he published a small paper on adaptations of freshwater gastropods (Russell Hunter, 1952) in which he formulated the concept that restricted freshwater habitats could lead to reproductive isolation of molluscan populations, and, therefore, development of intraspecific, interpopulation variation and physiological race formation. This hypothesis was to become the basis for much of his future research.

This paper was followed by a host of landmark papers on freshwater gastropods in 1953 (Russell Hunter, 1953a, b, c, d). One of these described the probable use of the mantle cavity gas bubble as a physical gill in *Lymnaea peregra* and for buoyancy in both *Lymnaea peregra* and *Physa fontinalis* (Russell Hunter, 1953b). Another involved a description of the seasonal migration patterns of *Lymnaea peregra* (Russell Hunter, 1953a). Use of the mantle cavity gas bubble as a physical gill and buoyancy mechanism was later described in detail for *Planorbarius corneus* and *Lymnaea stagnalis* by one of his graduate students, Andrew Henderson (1963).

In 1953 Dr. Russell-Hunter (1953c) also published an important paper on the growth rates, reproduction and population dynamics of a freshwater limpet, *Ancylus fluviatilis*. This paper was the first to indicate that the vast majority of freshwater pulmonates were annuals with one or two generations per year. More importantly, it showed that while the life cycle patterns of isolated populations were roughly the same (univoltine or bivoltine annuals) there was considerable intraspecific, interpopulation variation in growth rate and size at maturity and reproduction in reproductively isolated populations.

After the completion of these studies Dr. Russell-Hunter spent part of 1953–1954, studying the land snail fauna of Jamaica as a Carnegie and Brown (Royal Society) Research Fellow at the University of the West Indies, Jamaica. There he noted that while there was a large and diverse endemic land snail fauna, freshwater molluscs were represented by only a few cosmopolitan genera with a worldwide distribution. In spite of their low diversity, he observed that Jamaican freshwater molluscscan species displayed high levels of intraspecific, interpopulation variation. This observation along with his previous work on *A. fluviatilis* (Russell Hunter, 1953c) led him to hypothesize that the majority of freshwater habitats were not temporally stable enough to support the development of unique endemic species, but, instead, existed in geological time only long enough for genetically different races of the same species to develop (Russell Hunter, 1955, 1957).

On completion of his fellowship in Jamaica Dr. Russell-Hunter returned to The University of Glasgow to test these hypotheses in studies of populations of several species of freshwater gastropods in Loch Lomond. These studies eventually led to the publication of a pair of benchmark papers in the *Proceedings of the Zoological Society of London* that demonstrated the high degree of intraspecific, interpopulation life history variation characteristic of freshwater snail populations. It was in these papers that his ideas regarding the significance of intraspecific, interpopulation variation in freshwater molluscs were more completely formulated (Russell Hunter, 1961a, b). These papers demonstrated that while much of the variation observed in genetically isolated populations of freshwater gastropod species was induced by environmental differences such as temperature regime and food availability, some of the observed variation could only result from differences in their gene pools associated with adaptation to local microenvironmental conditions. Another early graduate associate of Dr. Russell-Hunter observed such genetically based, intraspecific variation in the morphology of the radular teeth of *Lymnaea peregra* (Berrie, 1959). Indeed, such variation in many morphological and physiological traits has been reported many times in publications resulting from research carried out in Dr. Russell-Hunter's laboratory over the last 20 years (Russell-Hunter, et al., 1967, 1981; Burky, 1971; Nickerson, 1972; Hunter, 1975a, 1975b; McMahon, 1975; Browne, 1978; Payne, 1979; Romano, 1980; Aldridge, 1982). Extensive discussions of the significance of such intraspecific, interpopulation variation appear in Dr. Russell-Hunter's three review chapters on freshwater molluscs (Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983).

In a recent conversation with one of us (RFM) just prior to this symposium, Dr. Peter Calow, a noted physiological ecologist from Sheffield University in England, stressed the importance of Dr. Russell-Hunter's discovery of apparently genetically based intraspecific, interpopulation variation associated with adaptation to microenvironmental conditions. Dr. Calow pointed out that it was one of the basic observations that eventually led directly to the development of modern theories of the evolution of life-history strategies and the optimalization of reproductive output. Not surprizingly, these subjects were major topics of these symposium proceedings.

In the 1960's and early 1970's Dr. Russell-Hunter's interest turned to studies of intraspecific and interpopulation differences in the population bioenergetics of freshwater molluscs and the marine pulmonate, *Melampus bidentatus*. He and his colleagues developed a wet ashing technique for determining tissue and shell organic carbon contents (Russell-Hunter, et al., 1968) that has recently been refined (Russell-Hunter, et al., 1982). Utilizing this technique, he and his graduate student associates began to study how populations of molluscs partitioned ingested energy into growth, reproduction and maintenance (catabolism measured as oxygen consumption) in investigations of the environmental and adaptational correlates of intraspecific and interpopulation differences in the efficiencies of production and reproduction of freshwater molluscan species (Apley, 1970; Burky, 1971; Mattice, 1972; Hunter, 1975a; McMahon, 1975; Avolizi, 1976; Browne, 1978; Browne and Russell-Hunter, 1978; Eversole, 1978; Payne, 1979; Aldridge, 1982; Tashiro, 1982; Tashiro and Coleman, 1982; for a review see Russell-Hunter and Buckley, 1983).

This research anticipated more recent studies of the bioenergetic analysis of life history adaptations by many years (for reviews of recent studies see Stearns, 1976, 1977; Charlesworth, 1980). Unlike many other studies of life history phenomena, Dr. Russell-Hunter and his colleagues not only presented hypotheses regarding the adaptive significance of observed life history traits, but, also, and perhaps, more importantly, provided the detailed, hard experimental evidence from natural populations of animals with which to test them (Russell-Hunter and Buckley, 1983). These studies of the bioenergetic analysis of life history traits in freshwater molluscs originated with pulmonates (Apley, 1970; Burky, 1971; Hunter, 1975a; McMahon, 1975; McMahon et al., 1974; Russell-Hunter and McMahon, 1976; Eversole, 1978; Romano, 1980) and sphraeiid clams (Avolizi, 1976). More recently he and his colleagues have concentrated their efforts on freshwater prosobranchs (Mattice, 1972; Brown, 1978; Payne, 1979; Aldridge, 1982; Tashiro, 1982; Tashiro and Coleman, 1982). Dr. Russell-Hunter is now turning his attention to life history adaptations in the freshwater unionids, many species of which are presently highly endangered by human activity, and for which very little experimental life history information exists.

Dr. Russell-Hunter, with his students and colleagues, has accumulated an extraordinary amount of bioenergetic data on the life history adaptations of freshwater molluscs (for reviews see Aldridge, 1983; Burky, 1983; McMahon, 1983; Russell-Hunter and Buckley, 1983). To collect such data is time consuming and difficult, but, it has now allowed him to much more rigorously test current hypotheses concerning the adaptive values of life history traits in freshwater molluscs than can be carried out for the vast majority of other groups of organisms.

Since the late 1960's Dr. Russell-Hunter and his graduate student associates have carried out an extensive series of transfer experiments. These experiments involve the analysis of intraspecific, interpopulation variation in the life history traits of isolated populations of freshwater molluscan species by transferring caged individuals between populations and observing changes that occur in their growth, reproduction and energy partitioning in relation to that of control individuals caged in the habitat of origin (Burky, 1971; Nickerson, 1972; Hunter, 1975a, 1975b; McMahon, 1975; Payne, 1979; Romano, 1980; Aldridge, 1982). These transfer experiments are highly labor intensive, but are one of a very few methodologies that allows accurate separation of non-genetic, environmentally induced variations in morphology, physiological responses and life history traits from those which result from genetic differences between publications. At the 1984 Society of Experimental Zoology Symposium on Physiological Ecology in Glasgow several investigators made a plea for such transfer experiments to be conducted in studies of interpopulation variation. Ironically, those of us fortunate enough to have been involved with his research in this area know that such transfer experiments have been a matter of routine operation in the laboratory of Dr. W. D. Russell-Hunter since 1967.

Dr. Russell-Hunter's most recent investigations have involved studies of the evolutionary and adaptive significance of the ability of freshwater pulmonates to degrow, that is to absorb structural proteins, during periods of starvation or reduced ingestion while overwintering or inactive (Russell-Hunter and Eversole, 1976; Russell-Hunter, et al., 1983, 1984; Russell-Hunter, 1985). Another continuing and important line of study has been the effects of food quality in terms of protein content on the partitioning of proteinaceous and non-proteinaceous compounds into growth, reproduction, and catabolism in freshwater pulmonate and prosobranch gastropods (McMahon, et al., 1974; Aldridge, et al., 1980; Aldridge, 1980, 1982; Tashiro, et al., 1980; Tashiro, 1982; Tashiro and Coleman, 1982). In addition to these investigations, his laboratory has recently completed an initial study of the neurosecretory controls of reproduction in the freshwater stream limpet, *Ferrissia rivularis* (Romano, 1980). Certainly, these most recent research efforts should be producing valuable new data on the evolution of physiological adaptations and life history traits in freshwater molluscs in the near future.

In addition to Dr. Russell-Hunter's many research contributions to the study of physiological ecology in freshwater molluscs, the following investigations have also been carried out in his laboratory: the biology and limnology of the Clyde Sea Area in Scotland (Russell Hunter, 1958); the mechanics of the hinge ligament of *Spisula solidissima* (Russell Hunter and Grant, 1962); the relationship between size and ctenidial number in chitons and its significance to theories of molluscan evolution (Russell Hunter and Brown, 1965); population density and dispersal in *Polinices duplicatus* (Russell Hunter and Grant, 1966); the mechanics of pedal expansion in *Polinices duplicatus* (Russell-Hunter and Russell-Hunter, 1968; Russell-Hunter and Apley, 1968); the life history, semi-lunar reproductive synchrony, physiological ecology, and hormonal control of reproduction in the salt marsh pulmonate snail, *Melampus bidentatus* (Apley, 1970; Russell-Hunter, et al., 1972; Price, 1977a, b, 1979, 1980; McMahon and Russell-Hunter, 1981); the adaptive significance of reverse metabolic acclimation in pulmonates (Burky, 1971; McMahon, 1973; McMahon and Russell-Hunter, 1981); the hormonal control of sex change in the protandry of the marine slipper limpet, *Crepidula fornicata* (Russell-Hunter, et al., 1971); respiratory response to hypoxia and temperature change in relation to the pattern of vertical zonation in intertidal snails (McMahon and Russell-Hunter, 1977, 1978); functional protandry in freshwater limpets (Russell-Hunter and McMahon, 1976); the effects of grazing by the intertidal snail, *Littorina littorea,* on periphyton standing crop, productivity and food quality (Hunter and Russell-Hunter, 1978, 1983); Effects of *aufwuchs* quality in terms of protein content on the growth and reproduction of freshwater snails (McMahon, et al., 1974);

and the study of parallelism and convergence in marine deposit feeding bivalves (Russell-Hunter and Tashiro, 1973, 1985). These studies, with those on freshwater molluscs described above, are representative of Dr. Russell-Hunter's broad range of interests in physiological ecology and malacology and have provided him with an unique overview of these subjects, rare in today's more narrowly focused research biologists.

Dr. Russell-Hunter's broad research experience in physiological ecology and malacology has culminated in four major review chapters (Russell-Hunter, 1964, 1978, 1983a; Russell-Hunter and Buckley, 1983) and the editing of a major Academic Press volume on the ecology of molluscs (Russell-Hunter, 1983b). In addition, he is the author of four books: *Aquatic Productivity* (Russell-Hunter, 1970) which contains one of the earliest descriptions of the significance of bioenergetic partitioning to the analysis of life history traits; *A Biology of Lower Invertebrates* (Russell-Hunter, 1968) and its companion volume *A Biology of Higher Invertebrates* (Russell-Hunter, 1969) which have now been translated into Spanish, Portuguese, Polish and Malaysian, and are read by students of invertebrate zoology throughout the world; and *A Life of Invertebrates* (Russell-Hunter, 1979), a major college textbook for the study of invertebrate zoology.

Dr. Russell-Hunter has also had a long and rewarding association with the Marine Biological Laboratory in Woods Hole, Massachusetts. He has been an independent investigator there for 24 consecutive summers and has carried out year long research programs there several times. He served as the Editor of the *Biological Bulletin,* published by the Marine Biological Laboratory, from 1968 to 1980. Under his editorship it gained in prominence as one of the preeminent general biological journals found in university and research libraries throughout the world.

In addition to his duties as editor of the *Biological Bulletin,* and four term member of the Board of Trustees of the Marine Biological Laboratory, Dr. Russell-Hunter was a lecturer in the Invertebrate Zoology Course at the Laboratory during the summers of 1961–1963. He was appointed director of the course from 1964–1968. During this period a large majority of graduate students in the United States interested in a research or teaching career in some aspect of invertebrate zoology took that course. Indeed, many of its graduates are now nationally recognized educators and scholars. Thus, Dr. Russell-Hunter was able to influence the training of nearly an entire generation of invertebrate zoologists in the United States.

Dr. Russell-Hunter's career as a scholar has been marked by the publication of 106 research articles. His research record becomes even more impressive when it is realized that this figure would rise to 173 if he followed the common practice of co-authoring research articles stemming directly from his graduate student's dissertation research. That so many of his students' papers, cited herein as coming from his laboratory, do not carry his name is an indication of his generosity and graciousness in this regard. Dr. Russell-Hunter has been recognized for his research efforts by election as a Fellow of both the Linnean Society and the Institute of Biology in 1957 and of the Royal Society of Edinburgh in 1965. He also now serves as a director of the Upstate Freshwater Institute in New York State.

Seventeen students have completed their Ph.D. degrees under Dr. Russell-Hunter's direction either in the United States (15) or Scotland (2). These students have taken positions in academics, and governmental and private research laboratories throughout the United States and Europe. Most of them continue to study various aspects of invertebrate physiological ecology, and the vast majority of those continue to work in malacology. If their published research, and now that of their own students is combined with that coming directly from the laboratory of Dr. Russell-Hunter, it becomes evident that he has had a very significant, world-wide impact on research in both physiological ecology and malacology, and on the teaching of invertebrate zoology over the last three decades.

As a final note, it should be mentioned that Dr. Russell-Hunter remains far from retirement. Therefore, we can expect that there will continue to be a steady stream of both new research and young research biologists coming from his laboratory (he is presently directing the dissertation research of three graduate students) for many years into the future. It is the hope of the organizers that this symposium in his honor will draw attention to new and important research areas in physiological ecology, particularly in the freshwater molluscs. However, perhaps the greatest honor that this symposium and these published proceedings could bestow on Dr. Russell-Hunter, would be that they stimulate other research biologists and their graduate students to focus their interests on modern research problems in physiological ecology.

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sonal honor for both of us to have been able to organize this symposium on his behalf.

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MECHANISMS OF LIFE HISTORY ADAPTATION IN THE TEMPORARY POND SNAIL *LYMNAEA ELODES* (SAY)

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ABSTRACT

Although intraspecific life history variation is often considered to have a genetic basis and to result from selection, there are other possible explanations. Here, I determine the relative importance of several components of phenotypic plasticity in life history variation among populations of the pulmonate pond snail *Lymnaea elodes* (Say): 1) differing levels of periphyton productivity, 2) physiological variation (divergence in tolerance to harsh environments), and 3) divergence among populations.

Habitat primary productivity is the major contributor to intraspecific life history variation in this vernal pond snail. Snails reared in the more productive pond grow roughly twice as fast and lay nine times as many eggs. Plasticity is greatest for fecundity, and less for growth traits. Vernal pond snails differ somewhat from snails originating from permanent ponds, in two ways. First, they mature at an earlier age and a smaller size, have slower growth, greater fecundity, and die earlier no matter which pond they are reared in. Second, life history traits are more canalized to harsh environmental conditions than in snails from permanent ponds. Thus physiological and developmental mechanisms (tolerance to stress) are just as important in life history adaptations in *Lymmaea elodes* as are genetic mechanisms.

Intraspecific variation (e.g. phenotypic plasticity) in life-history patterns and its relation to natural selection is currently an important topic in evolutionary biology (Stearns, 1976). However, there are various modes of life-history adaptation, not all of them strictly genetically based (Stearns, 1980). For example, one can partition the phenotypic plasticity of life-history traits into several components (Fig. 1). Variation among and within populations can be genetically set within narrow limits. All of the "theories" of life-history evolution (r- and K- selection, bet-hedging, etc.) that were espoused during the late sixties and early seventies assume some amount of genetic variation in life-history traits as well as genetic covariation among them (Stearns, 1976; 1980; 1984).

However, traits can also show broad expression subject to the influence of environmental factors (Fig. 1). For example, Berven (1982a,b) found that populations of wood frogs in ponds separated along an altitudinal gradient differed in their life histories. Although there was a detectable genetic component, most of the variation was explained by declining average water temperatures in the higher elevation ponds. For Lymnaeid snails there is some evidence of genetic variation in life histories (Forbes and Crampton, 1942; Russell-Hunter, 1978; Calow, 1981; Brown et al., 1985). In addition, for *Lymnaea elodes,* there is abundant evidence that proximal variables can affect life-history traits. *Lymnaea elodes* is primarily a microherbivore on periphyton (Brown 1982). Eisenberg (1966) used field manipulations to show that adult fecundity as well as juvenile growth and survival were sensitive to adult density, and argued that micronutrients in the algal food sources were limiting. Hunter (1975) found considerable variation among populations in voltinism patterns and in production rates, and considered that habitat productivity was a major causal factor. Brown et al. (1985) found that individuals completed their life cycle in one year in productive ponds, but took 2 or possibly 3 seasons in less productive, temporary ponds.

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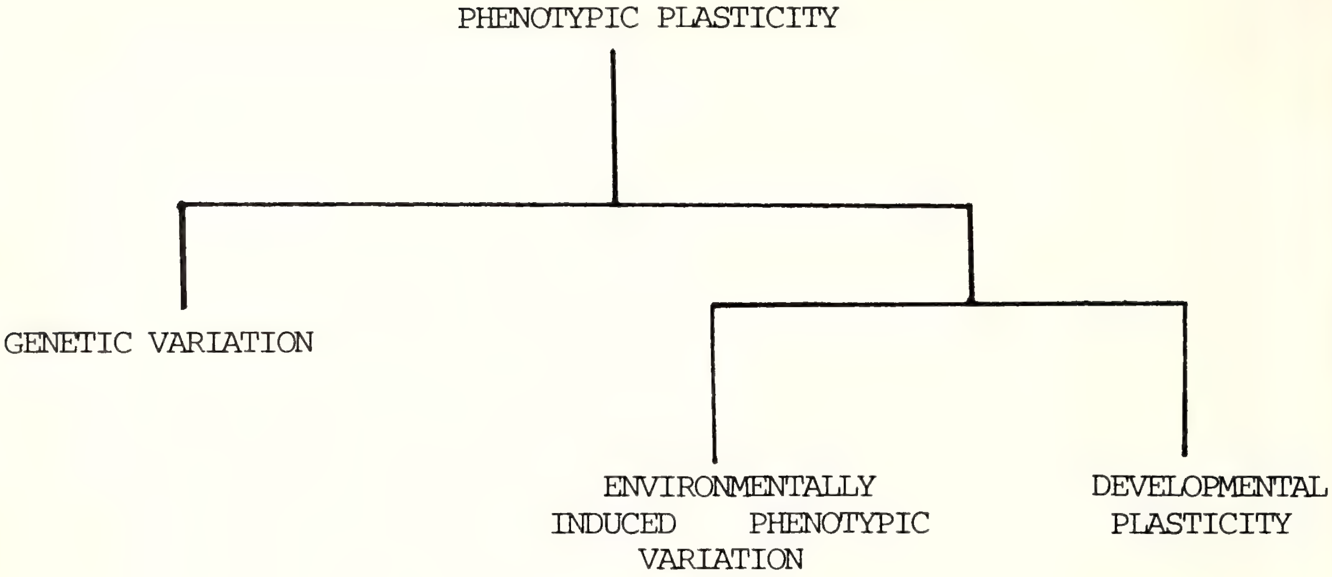

Fig. 1. The components of phenotypic plasticity in life-history traits.

Although usually slighted in theoretical treatments, physiological and developmental responses (e.g. changes within the life cycle of individuals) can also explain much of intraspecific life-history variation (Stearns, 1980). For example, the degree of canalization of expression can vary among populations and traits, or even for the same trait at different ages. Likewise, individuals may physiologically differ in tolerance to environmental extremes.

In this paper, I study intraspecific phenotypic plasticity in the life-history of the pond snail *Lymnaea elodes*, with three objectives in mind. First, I compare the relative importance of proximal variables (specifically habitat productivity and adult density), and population divergence in explaining life-history variation among three pond populations in north-eastern Indiana, USA. Second, I compare the degree of canalization of several life-history traits, and how levels of canalization vary among vernal and permanent pond populations. The term canalization is used here to refer to the degree of inflexibility of life-history traits to experimental manipulations. Finally, I consider how the ability to physiologically withstand stress may in itself be adaptive in vernal pond snails.

MATERIALS AND METHODS

Description of the Ponds

Ponds A, B, and F are within a 30 km radius of the Crooked Lake Biological Station of Purdue and Indiana Universities, about 33 km north-west of Fort Wayne, Indiana, along the southern border of Noble County. The ponds are similar in most physicochemical variables (temperature, pH, dissolved oxygen) but differ both in permanency and productivity (see original data in Brown 1982, Brown et al., 1985). Pond B has the hardest water, but the lowest periphyton biomass, as measured on slides suspended in the ponds (Brown et al., 1985). Pond A has intermediate levels of periphyton biomass, but is the most temporary of the three ponds (drying anywhere from early June to late August, depending on weather, while pond B does not usually dry until late in August). Pond F is a permanent pond, and has the highest rates of periphyton accumulations on slides, as well as dense associations of submerged macrophytes.

Experimental Methods

Two field manipulations are described in this paper. The first was conducted in the summer of 1980, and involved transferring immature snails among the ponds. A second experiment compared the life-history variation of parents and their offspring from two populations reared in the same pond, and was conducted in 1981 and 1982. Rearing methods were fairly similar in both experiments. Snails were reared in 1 L plastic tubs with screened holes to allow water circulation and retard container effects (Brown et al., 1985). Juvenile snails (averaging 5 mm in shell length, and ranging from 3 to 7 mm) were placed in the containers during the first week in May at the specified densities. The containers were attached to floats to assure adequate oxygen for the snails. Rearing methods are discussed in more detail in Brown (1982), and Brown et al. (1985).

Transfer Experiment

This experiment was designed so that snails from the most vernal pond (pond A) were compared with native populations in each pond (with the exception of pond A where snails from pond F were used). The snails were also reared at two densities, 2 and 4 snails per container. Thus the design contrasted the effects of habitat productivity (the pond effect), density, and source population (comparison of pond A to other populations). There were 15 replicate containers in each of the 12 treatments for a grand total of 180 containers (60 in each pond). For each container, data were averaged over all snails on age (days since the start of the experiment when eggs were first found in the container) and shell length at maturity (the average shell length of all snails in the container when eggs first appeared), growth increment, total fecundity, and mean number of eggs per mass (clutch size). Since snails were stocked in containers at different initial sizes, the averaged data were subjected to an analysis of covariance (with initial average shell length of the juveniles) with a factorial arrangement of treatments. Since the same 2 populations were not reared in each pond, the factorial design is an incomplete $3 \times 2 \times 2$, hard to statistically analyze. I therefore analyzed all data in a simpler 2 ponds (A and F) × 2 populations (A and F) × 2 densities design. I have still included pond B rearing results in the figures, since it is the least productive pond, and clear trends across ponds are evident in most cases. I consider the $2 \times 2 \times 2$ design to be conservative due to its lower number of degrees of freedom, and therefore consider the same treatment effects, at least, would be significant if pond B were included in the analysis, increasing the error degrees of freedom. Probability values reported in the results refer to either the main effects (habitat productivity/pond effect, density, or source population) or the covariate (initial shell length) in the $2 \times 2 \times 2$ covariance analysis.

Parent-Offspring Experiment

In the second experiment, snails from both pond A and the permanent pond (hereafter referred to as parents or P generation) were reared in the permanent pond in 1981, and their eggs collected and maintained in the laboratory at 5 C to retard growth until the next spring. The offspring (hereafter referred to as F_1) were then reared in the same pond in 1982. All F_1 offspring from a single P individual are referred to as a family. The permanent pond was selected because premature drying would not preclude measuring physiological ages and shell sizes at death, and because pond F's greater productivity would overide food limitation of life-history traits. I attempted to keep juvenile densities as low as possible in aquaria during the overwintering, but for P adults with high fecundities, F_1 individuals probably underwent some density-dependent stress, as discussed later.

Statistical analyses were again analyses of covariance with initial size, with a factorial arrangement of treatments (2 populations times 2 generations). In some cases, coefficients of variation (standard deviation / mean × 100) are compared across treatments or families.

RESULTS

Transfer Experiment

Habitat productivity had a marked effect on age at first reproduction, with snails maturing in about 42 days on the average in pond F, 50 days in A, and 60 days in B (Fig. 2, $p < 0.001$, e.g. the habitat effect F value was significant at the 0.1% level). Increased rearing density delayed age at maturity (Fig. 2, $p < .05$). The source population effect was not significant ($p = .06$), although the covariate, original shell length, did significantly affect age at maturity ($p. < .01$).

In contrast, all of the main effects were highly significant for shell length at maturity (Fig. 3). Averaged over both source populations, snails matured at only 15.5 mm shell length in pond B, at 18 mm in A, and at 19 mm in F (habitat effect, $p < 0.001$). Increased density lowered shell length at maturity by about 5% on the average ($p < .01$). Pond A snails matured at shell lengths on the average about 84% of those of comparison populations ($p < 0.001$). The covariate, initial shell length, did not have a significant effect ($p = .06$).

Similarly, shell growth increments were highly significantly affected by habitat productivity ($p < 0.001$), source population ($p < 0.001$), and density ($p < 0.001$, Fig. 4). Snails grew roughly 6 mm after maturity in pond B, 7.5 mm in A, and 11 mm in F. Doubling snail density caused a 16% reduction in shell growth, overall ponds and populations. Pond A snails had shell growth increments that were on the average 78% of comparison populations. The covariate did not have a significant effect.

The average number of eggs produced per adult was markedly higher in the more productive, permanent pond (Fig. 5, $p < .01$). Snails laid on the average about 30 eggs per adult in pond B, 40 in A, and 230 in F. Pond A snails laid on the average about 1.8 times as many eggs as comparison populations ($p < .05$), and a doubling in density depressed fecundity on the average by 71% ($p < .01$). Initial size had a highly significant effect ($p < 0.001$).

Clutch size also increased significantly with increasing habitat productivity (Fig. 6, $p < 0.05$), from 16.3 in pond B, to 19.5 in A, and 23.0 in pond F. A doubling in density significantly decreased clutch size ($p < 0.001$) by an average of 21%. Source population did not however have a significant effect. The covariate did not have a significant effect.

Canalization of Traits

To gain an idea of the relationship of plasticity in traits to habitat productivity, data from the transfer experiment were averaged over all source populations and densities, and coefficients of variation were calculated for each trait (Table 1). Although different populations were reared in each of the ponds, several trends were still clear. For example,

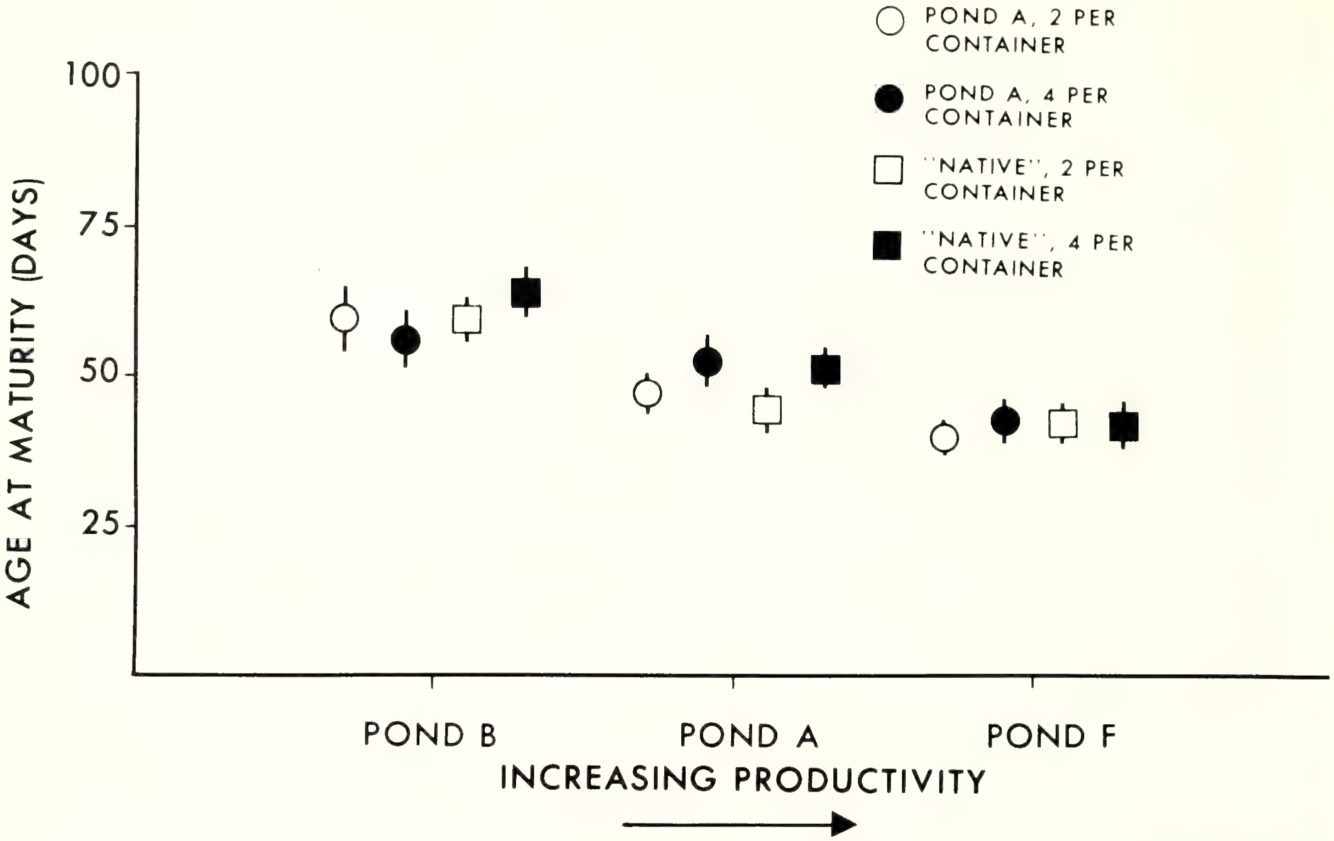

Fig. 2. Habitat dependent changes in age at maturity (days since start of the experiment). Data are means ± s. e. ($n = 15$). "Native" populations were used for comparison to Pond A snails, except of course in pond A, where snails from pond F were used. Circles refer to snails originally from pond A, squares to comparison populations. Dark symbols are containers with 4 snails, light symbols, 2 snails.

note that variation is greater for some traits than others. Total fecundity is the most variable, followed by clutch size, and growth increments, with age at maturity and shell length at maturity the least variable. Phenotypic variation also decreases as habitat productivity increases, particularly for age at maturity, growth increment, and clutch size (Table 1). Thus higher levels of habitat productivity are accompanied by a reduction in population and density effects, except in the case of shell length at maturity, which shows a low but stable level of variation in each of the three ponds (Table 1).

In the parent-offspring experiment, coefficients of variation were also calculated for each of the F_1 families with more than one offspring reared (Table 2). These data also illustrate the degree of variation among the examined life-history traits. Fecundity again is highly variable, while most of the other traits show intermediate levels of variation among families, usually ranging from 25 to 35 per cent. The traits showing the least phenotypic plasticity are again shell length at maturity, and also shell length at death. Averaged over all seven traits in Table 2, there was no significant difference between source populations in degree of phenotypic plasticity ($t = .19$, $p = .14$), indicating no genetic divergence for canalization of traits.

Tolerance to Density-dependent Stress

As mentioned in the methods, overwintering procedures may have introduced some degree of density dependence to the expression of traits in the F_1 offspring reared in 1982. Interestingly, F_1 offspring originating from the permanent pond showed more of an average drop in fitness traits (22%, Table 3) than vernal pond snails (8.3%). Averaged over all traits, the difference was significant at the .05 level (Table 3). Note also that drops in fecundity-related traits were generally greater than for growth-related traits, again indicating less canalization. Although yearly environmental variation could also explain such differences, comparison of physico-chemical data (Brown, 1982) showed at least no obvious difference between the two ponds in 1981 and 1982.

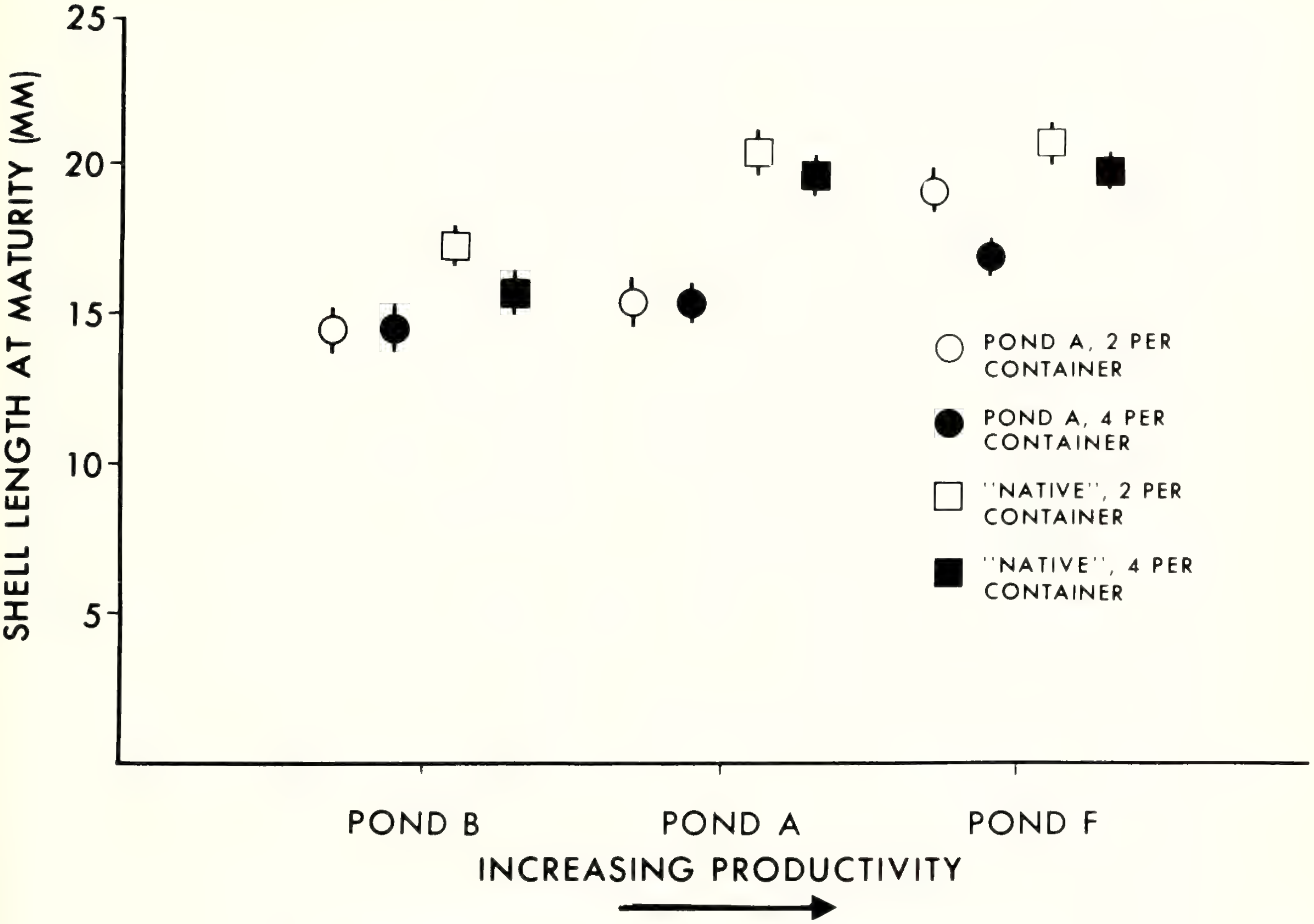

Fig. 3. Habitat dependent changes in shell length at maturity. Symbols are as in Fig. 2.

DISCUSSION

As suggested in previous studies of *Lymnaea elodes* (Eisenberg, 1966; Hunter, 1975), environmental variables such as habitat productivity and population density have dramatic effects on life-history traits. Brown et al. (1985) found that *L. elodes* populations in less productive, temporary ponds have poor survivorship in years when the pond dries early. However, density dependence (e.g., a reduction in per capita fecundity) occurs in years when the pond remains full for most of the season, due to the higher levels of recruitment, and lower primary productivity in comparison to more productive, permanent ponds.

Genetic divergence among populations is relatively small, but still significant for some traits. In comparison to snails from permanent ponds, temporary pond snails reproduce at an earlier age and smaller size, grow more slowly, and produce more eggs, regardless of the environment they are grown in. Although these divergences are small, they still may be important in an evolutionary sense. That is, since selection differentials are usually considered to be relatively small in natural populations, and to act over long intervals to produce divergence, these small divergences are what would be expected to result. In Brown et al. (1985) we suggest the adaptive nature of the divergences lies in allowing snails in vernal ponds to reproduce at the earliest possible age, which is obviously important in an unpredictable environment.

The fact that life-history traits vary in their degree of canalization has important evolutionary implications. In *L. elodes*, several different analyses suggest that fecundity related traits vary more than traits such as age and size at maturity. While this result at first seems paradoxical, it may be explained again by the unpredictable nature of the environment *L. elodes* is found in, vernal ponds (Brown, 1982). In an environment where the length of the reproductive season is highly variable from year to year, the better strategy

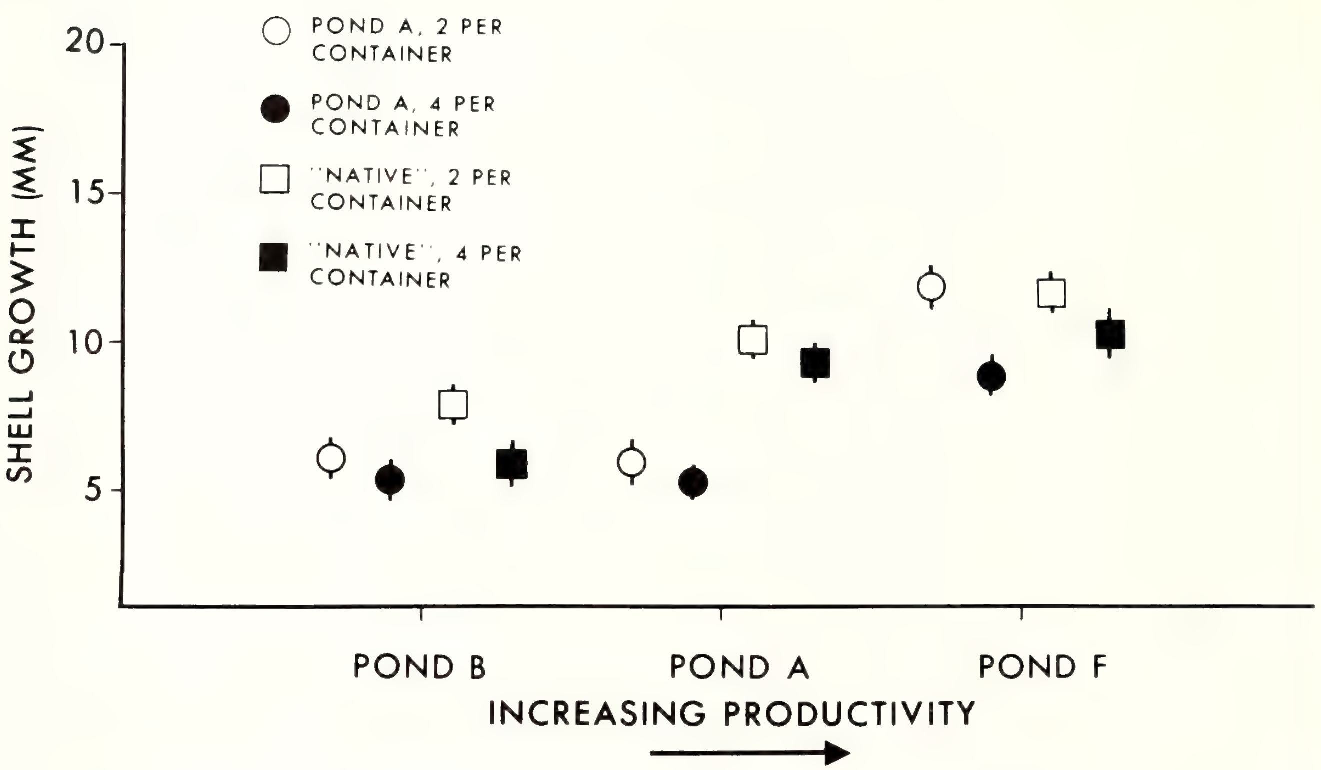

Fig. 4. Habitat dependent changes in total shell growth. Symbols as in Fig. 2.

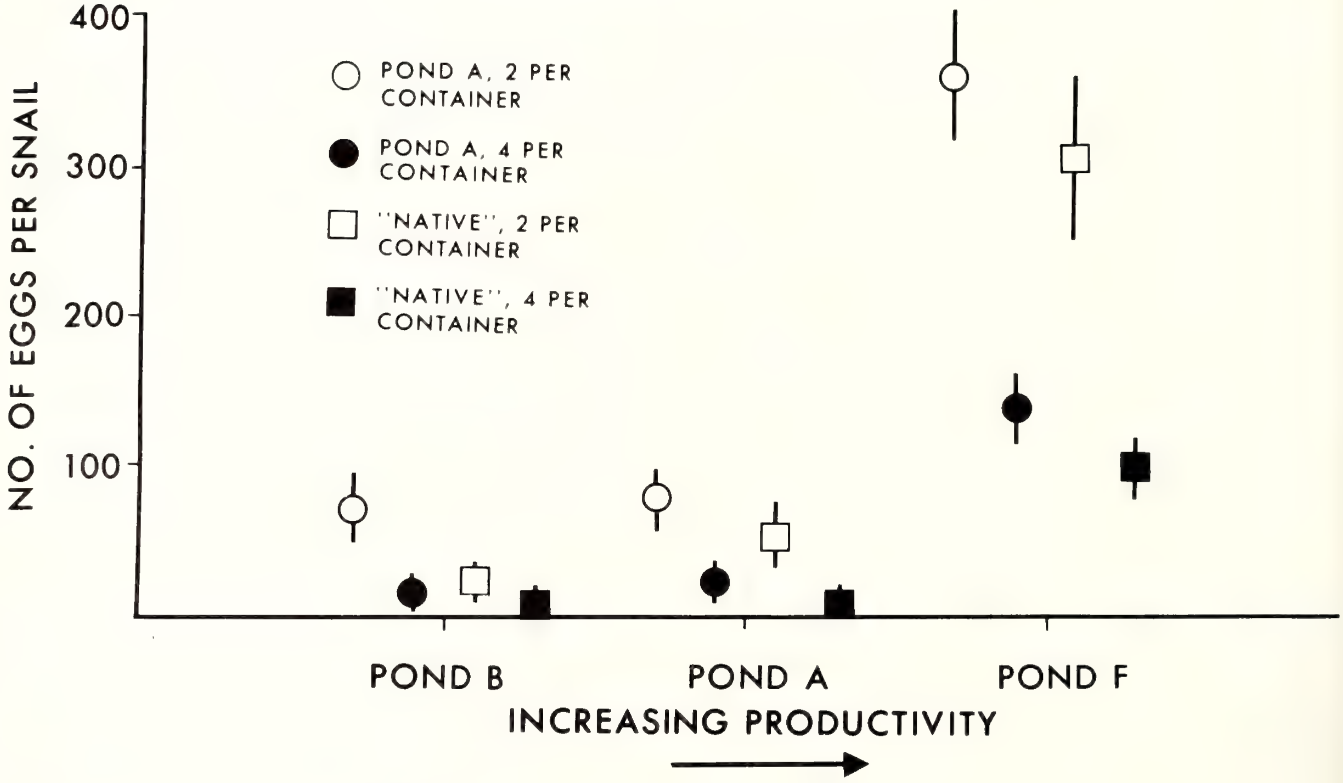

Fig. 5. Habitat dependent changes in total fecundity. Symbols as in Fig. 2.

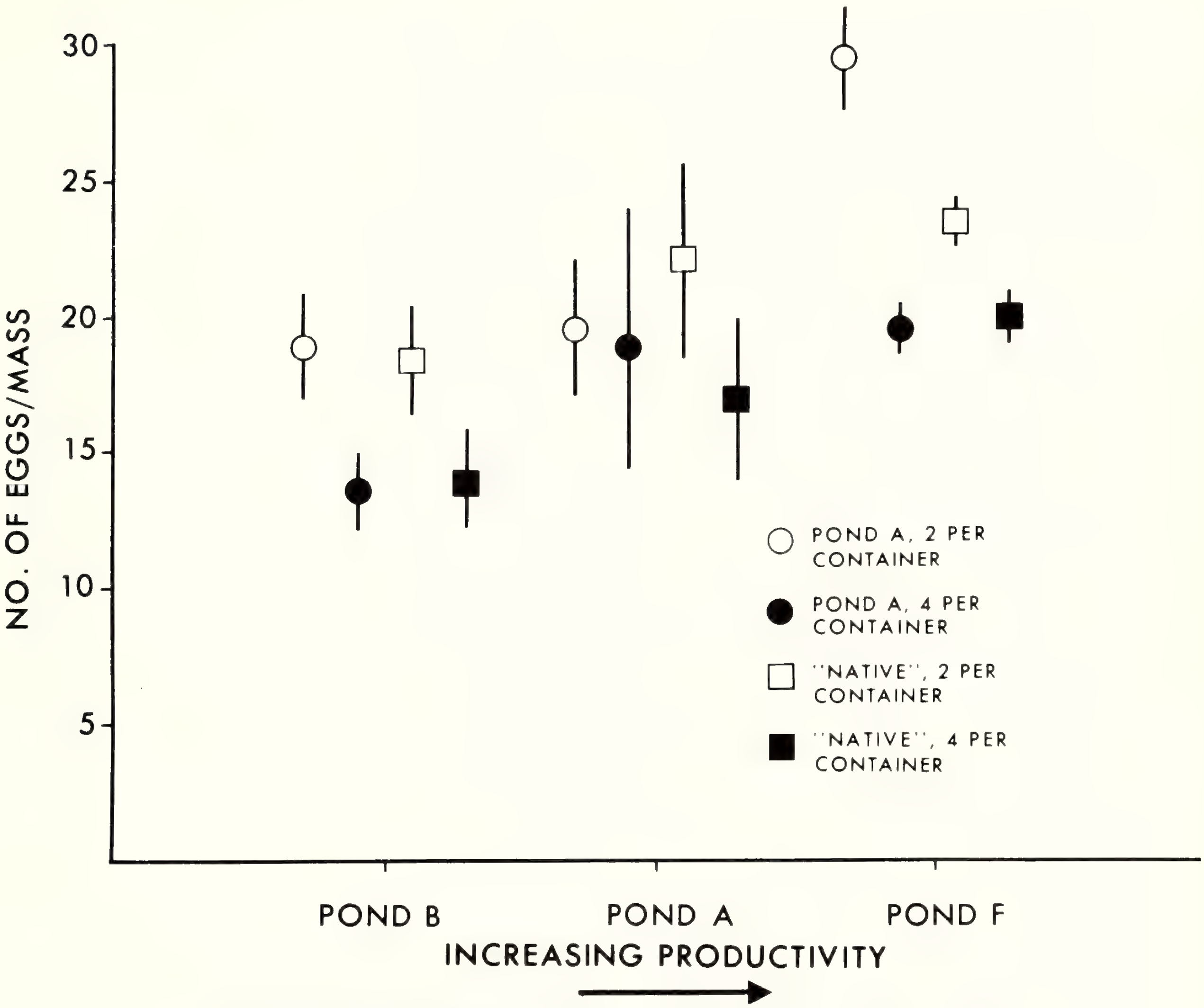

Fig. 6. Habitat dependent changes in the number of eggs per mass. Symbols as in Fig. 2.

Table 1. Coefficients of variation (S.D./$\bar{X} \times 100$) for snails reared in each pond during the transfer experiment. Data were averaged over source populations and densities.

	POND		
	B	A	F
Age at Maturity	14.0	16.8	3.7
Shell Length at Maturity	8.7	9.6	9.6
Growth Increment	35.5	28.8	22.5
Total Fecundity	65.1	63.3	54.0
Clutch Size	29.5	48.8	22.9

may be to maximize growth to ensure early reproduction, rather than to concentrate on high levels of reproduction. This would assure some reproductive success, even in years when the pond dries at an early date. Since snails from both the temporary and permanent pond showed similar coefficients of variation for traits, canalizing selection has evidently focused on growth related traits even in the permanent pond. Perhaps a minimum size is necessary for reproduction, and growth is maximized to that shell length, after which energy is diverted to either growth or reproduction.

Finally, the greater resistance to physiological stress in the temporary pond snails may also be important. Theories of life-history evolution have concentrated primarily on what

Table 2. Coefficients of variation (± s.e.) for families from ponds A and F, reared in pond F in 1982.

	POND	
	A	F
Age at Maturity	25.9 ± 2.6	30.9 ± 6.1
Shell Length at Maturity	10.9 ± 1.1	8.6 ± 1.5
Growth Increment	36.7 ± 3.2	32.9 ± 3.9
Total Fecundity	63.6 ± 6.1	60.3 ± 4.2
Clutch Size	25.5 ± 2.4	27.4 ± 2.5
Age at Death	32.5 ± 3.9	25.5 ± 2.4
Shell Length at Death	15.4 ± 1.2	12.9 ± 1.1
Sample Size (Number of families with more than one offspring)	13	11

Table 3. Percent reduction in F_1 averages for life-history traits with respect to P values for both populations.

	POND	
Trait	A	F
Age at Maturity	11.0	44.2
Shell Length at Maturity	1.0	9.4
Growth Increment	9.3	21.4
Total Fecundity	13.0	31.3
Clutch Size	19.2	32.2
Age at Death	5.9	13.5
Shell Length at Death	− 1.0	2.3
Average	8.3	22.0
t Value	2.22 ($p<.05$)[1]	

[1] over all traits, see text

traits, and associations of traits are selected for in specific environments. The current results indicate that the ability to resist environmental extremes in unpredictable environments may be selected for as well, and this idea needs to be incorporated into current theories of life-history evolution.

ACKNOWLEDGEMENTS

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ENERGY PARTITIONING AND ECOLOGICAL PLASTICITY IN POPULATIONS OF *ANCYLUS FLUVIATILIS* (GASTROPODA: BASOMMATOPHORA)

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ABSTRACT

Energy partitioning studies in *Ancylus fluviatilis* were performed using artificially prepared periphyton layers of algae labelled with ^{14}C. Due to the morphometric dimensions of the radula's scraping mechanism and the inherent maximum speed of grazing, ingestion is possible only on periphyton layers between ca. 0.1 and 2 μg C/mm^2. The lower the concentration, the more time is spent grazing in order to ingest the daily energy amount needed. Below 0.1 μg C/mm^2, food is not accepted, since grazing at such low concentrations would not provide the energy demands needed. Time periods available for non-grazing activities are a function of the local algal thickness and are used for either resting or migrating periods, the latter roughly according to a random walk. The limpets exhibit variable preferences, which are a function of temperature, for the top or bottom of stones. Studies on the internal economy showed that production efficiency is high in young sedentary individuals. Large individuals are less sedentary and are less efficient energy converters. Only at actual time of spawning is efficiency relatively high again. High temperatures cause high losses of respiration energy, mucus, and released dissolved organic material, and make the limpets inefficient and probably poor competitors. This explains why they are found preferentially in cool-river systems. The high costs of extended locomotory activities will probably be minimized in populations where this trait is not selected for. Field observations indicate that different populations differ in the percentage of energy allocated for either locomotory activities or reproduction.

An individual at any age x can allocate a fraction of its available energy resources to reproduction and the remainder to maintenance (or survival) and growth. We can call this fraction the reproductive effort at age x (Charlesworth, 1980). For many organisms the available energy resources are not a fixed quantity. Local populations may genetically be selected for how much energy its individuals will gather. By foraging for energy to be used for reproduction, the animal exposes itself to increased mortality, either through predation or the threat of local overgrazing. The tradeoff between survival and reproduction may thus be determined by this selection (Abrams, 1983). The strategy adopted by individuals in a population has an effect on the food resources which, in turn, may have a feedback effect on the optimal strategy of a given individual.

To date, empirical studies of resource partitioning and niche structure have been concerned largely with "input" phenomena and have neglected to relate these to "output" aspects. Studies of reproductive tactics have done the reverse and almost entirely omitted any consideration of foraging (Pianka, 1983).

This study tries to merge aspects of optimal foraging with optimal reproductive and energy allocation tactics in the freshwater limpet *Ancylus fluviatilis* O.F. Müller 1776, to specify how input is translated into output. This involves consideration of foraging and ingestion processes, internal economy and energy partitioning, and energy output, such as in tissue growth and egg production. Any quantitative data on energy partitioning will have to take into consideration the specific local life-history traits. Besides experimentally based data, field data were collected also to aid the interpretation of the experimental results.

Direct energy-flow data, based on the fate of ^{14}C labelled food, represent the most direct method of measuring energy uptake and allocation patterns under different conditions. Earlier studies have shown that the energy conversion from assimilation into growth and egg production is low (Streit, 1975a,b; 1976b,c). The present study focuses on results of those experiments together with new results on aspects of nonproductive energy uses, such as locomotory activities. An hypothesis will be presented which explains the low production efficiency of *A. fluviatilis* populations on the basis of high energy costs for dispersal in search of local grazable habitats, and also on the basis of endogenous inactive periods.

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BIOLOGY AND LIFE-HISTORY

Ancylus fluviatilis is found in lotic freshwater environments throughout Europe from the Caspian Sea to Ireland, and from Southern Scandinavia to North Africa (Hubendick, 1970). It usually has an annual life-cycle (Russell Hunter, 1953, 1961a; Lamberet 1966; Streit 1974, 1976b). Eggs are laid within capsules containing 1–13 eggs (most frequently 4 to 6; Geldiay 1956 and others). Egg laying in spring is initiated when ambient temperatures reach 7–10 °C. Roughly 10 to 20 egg capsules are deposited by each individual over the entire life-span (Russell Hunter, 1953; Geldiay, 1956; Lamberet, 1966). Hatched juveniles have a shell aperture length (AL) of 0.8 to 1 mm (Lamberet, 1966) and a carbon content of ca. 6.6 μg C (value for 1 mm AL; Streit, 1975a). Egg-laying often starts at an AL of 5 mm and 477 μg shell-free carbon content; Streit, 1975a), but populations differ slightly in this respect. Maximum observed length in Central European populations is about 11 mm (Streit, unpublished), but in most populations of this area, the maximum length does not exceed 6–8 mm.

Shell form and thickness variation is great, especially between populations, and was originally a reason to subdivide the species into subspecies and varieties. Not many quantitative data are known about interpopulation variations of ecophysiological characteristics, but such traits as mean number of egg capsules per adult, time of maximum activity and spawning, and the necessity for cross-fertilization vary between populations (Russell Hunter, 1961b; Streit, 1975a, 1976c). Interpopulation variations in other ancylid limpets were studied by Russell-Hunter et al. (1970), Burky (1973), and McMahon (1973). Copulation did occur in field animals, but was not obligatory in our experiments, indicating self-fertilization to be possible, although other reports (e.g., Bondesen, 1950, in Danish populations, and Geldiay, 1956, in British populations) claim cross-fertilization to be necessary. Egg masses are deposited primarily during night-time (Berg et al., 1958) beneath stones (Geldiay, 1956).

Population densities vary strongly both within and between populations, with values from below 3 per m^2 up to 2000 per m^2, the latter at hatching times (Russell Hunter, 1953, 1961a; Maitland, 1965; Streit, 1976b and unpublished). Inter-annual fluctuations in densities are great in many populations.

The species feeds on periphyton material on smooth stone and rock surfaces and alternates periods of feeding (mostly of diatoms and green algae; Schwenk and Schwoerbel, 1973; Streit, 1975a; Calow, 1973, 1975), with locomotory activities on the top of stones and resting periods at the bottom sides (Streit, 1981).

Many populations carry several individuals of an oligochaete worm, *Chaetogaster limnaei limnaei,* per limpet individual, which live as harmless epizoic animals on the mantle area. They are found in many Central European lowland populations and in British populations (André, 1891; Geldiay, 1956; Streit, 1974), but, e.g., not usually in Black Forest populations. Another invertebrate species associated with *A. fluviatilis* is the larva of the chironomid *Eukiefferiella* sp., reported from British populations (Geldiay, 1956). Nematodes have been found within hemolymph lacunae (André, 1891). The outer shell areas are often covered with protozoans, such as *Vorticella* sp.

The only other ancylid species occurring naturally in Europe is *Ferrissia wautieri,* restricted to warmer areas and apparently not co-occuring with *Ancylus fluviatilis.* Main food competitors of *A. fluviatilis* are probably insect larvae, such as those of mayflies and stoneflies. Young specimens suffer from predation losses by stonefly larvae and other invertebrates. Occasionally, fish species like salmon, trout, minnow, and three-spined stickleback eat limpets, too (e.g., Maitland, 1965). The only notable predator of medium-sized to full-grown individuals in our study area seemed to be a leech, *Glossiphonia complanata,* able to reach the soft parts of the limpet by penetrating between the shell and the rock surface. In many populations, however, density independent factors, such as destructive floods after spring snow melt are probably primary causes in density control.

MATERIALS AND METHODS

SAMPLING LOCALITIES

The sampling sites were two running-water systems in the Western Part of the Lake Constance area (at the 3 corner point of West Germany, Switzerland, and Austria, Fig. 1). Populations I-III are located within a single, originally connecting, system (In recent times, a man-made small waterfall and pollution separated I and II from III). They lie just outside the farthest end moraines of the last glaciation period and could have persisted since inter-glacial times, although both chemical and physical characteristics, such as temperature and size of the river, must have undergone severe alterations through time; even the flow of the river was reversed during the ice age. Population IV is located within a drumlin landscape which was ice-covered in top-glacial periods. This population is therefore definitely of late or post glacial origin with no present-day connection to other populations. No specimens occur in Lake Constance, possibly because of the high sedimentation rate to the bottom rocks, or because suitable coherent smooth rock substrata are not usually found in adequate water depths. The high temperatures of up to more than 30 °C in littoral zones in summer prevent this area directly from colonization.

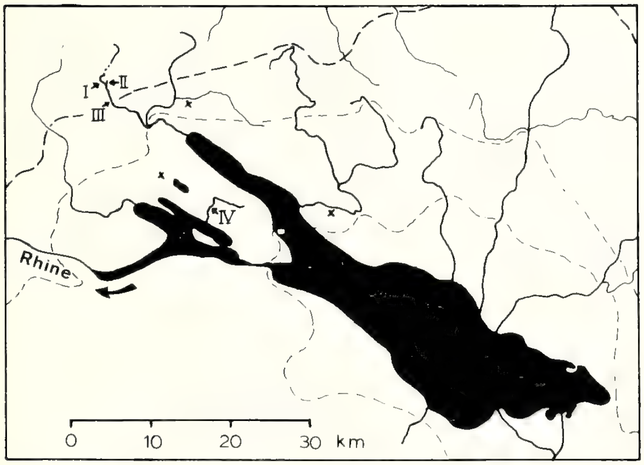

Fig. 1. Site of populations I through IV in the Lake Constance (Bodensee) area. Maximum alpine Würm glaciation (end moraines at the bold dashed line), covering site IV under ice, as well as two later moraine belts are shown. Several other populations of *Ancylus fluviatilis*, though usually not large in individual numbers (some sites indicated by a cross), live in other northern tributeries of Lake Constance.

Present-day elevations above sea-level (450–500 m) and Ca^{2+} concentrations (80–86 mg/l) are similar at all sites, but temperature regimes as well as many biological characteristics are markedly different. Population I and II are both located only a few hundred meters downstream from a subterranean portion of the respective river systems experiencing very low temperatures in summer, and only moderately cool ones in winter. Populations III and IV live in more typical thermal environments (Table 1). Two photographs of the habitats of populations I and III are provided in Schröder and Streit (1983; Fig. 3 and 4, respectively).

FIELD SAMPLING

Limpets were collected quantitatively (on a square meter basis) at least once a month. The microenvironmental site of each individual collected (such as linear dimensions of the stone and whether it was encountered on top, sides, or bottom of the stone) was always recorded. Shell dimensions of the limpets were measured in the laboratory. In addition, individuals to be used for experimental studies were collected and kept in isolating containers. These limpets were also measured before using and then placed on artificial periphyton in experimental flasks for acclimation to experimental conditions, as described below. All size classes found at the time of collection were used and different temperatures chosen. The majority of experimental studies were performed with population I individuals, whereas the others were used for comparison only. Field studies were performed with all four populations.

Variation in natural periphyton concentrations at the four sites was measured by taking individual stones into the laboratory, scratching off areas of 1 cm^2 with a blade, and transferring the algae into a vessel of water. From there, they were transferred onto diatomaceous earth in the way described in the "techniques" section for algal suspensions.

EXPERIMENTAL DESIGN (Fig. 2.)

An artificial laboratory system of four 6 m channels (Streit et al., 1978) was used to keep an animal stock, origi-

Table 1. Environmental and biological characteristics of Populations I-IV. I-III occur within the same river system (I and II very close to each other and easily mixing, III about 2 km downstream), IV in a system that may have been fully separated from I-III during the whole postglacial period. They lie all at around 450–500 m above sea level.

	I	II	III	IV
Highest temperature in summer in °C	11.8	12.6	21.5	20.8
pH (spring, noon)	7.5	7.3	8.3	7.6
Calcium in mg/l (spring)	84	81	80	86
Organic Pollution	low	low	mean/high	low/mean
Total Primary Productivity (estimate)	high	low	high	mean
Dominance of Cladophoraceae in summer	+	–	+ +	–
Percentage of grazers in macroinvertebrate populations on rock surfaces	25–70%	over 80%	7–45%	over 80%
Mean population density (all ages) as limpets/m^2	316	107	44	304
Mean biomass in mg C/m^2	65	27	27	38
Estimated ingestion of population (in mg C/m^2 · life span)	3044	1455	1209	3544
Estimated assimilation of population (in mg C/m^2 · life span)	1526	719	617	1934
Total eggs per adult limpet	66	–	–	113
Predation by *Glossiphonia complanata*	+	?	+	–
average shell dimensions as (height × width)/$(length)^2$	0.29	0.30	0.30	0.33*

[* = significantly different from the others]

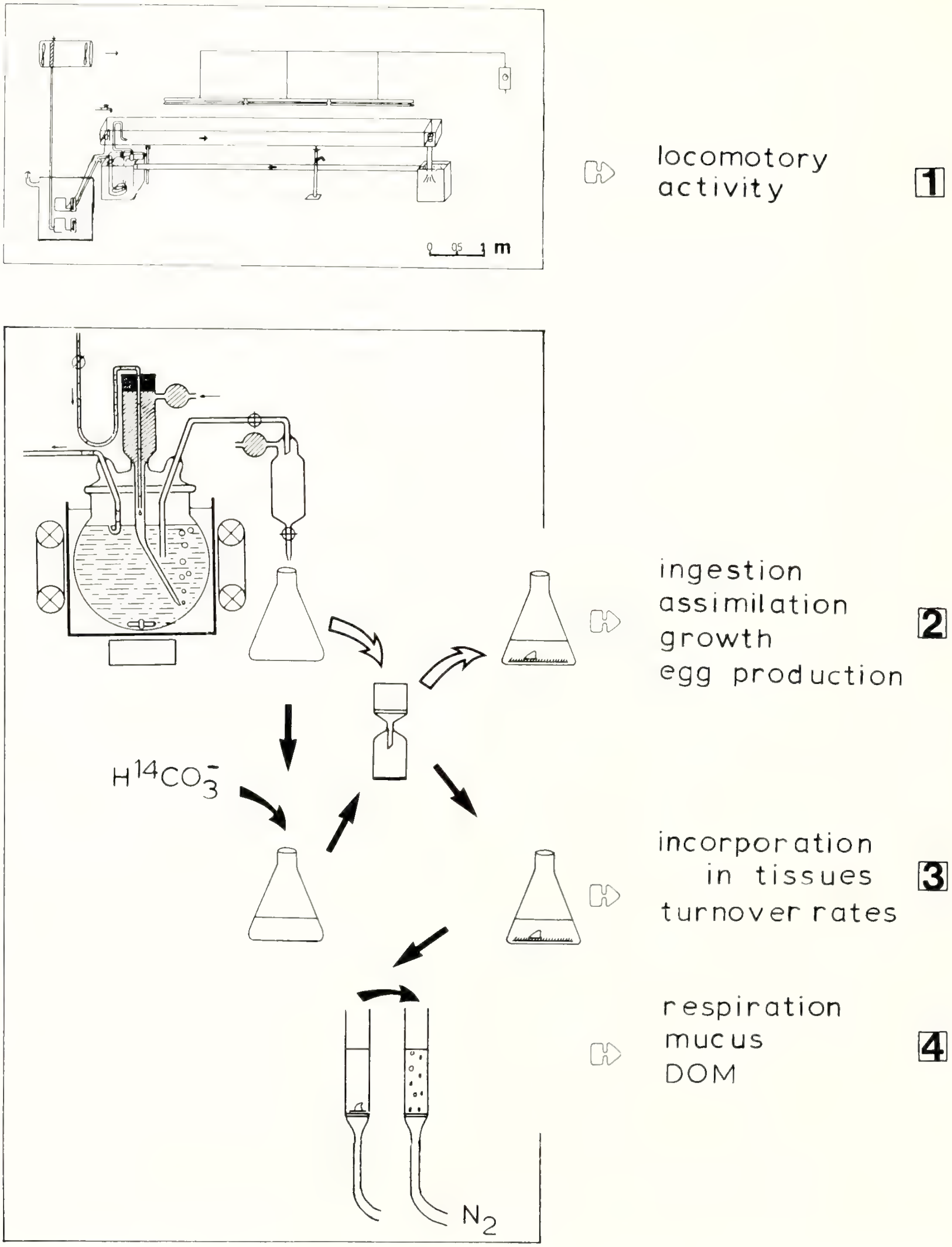
0 0.5 1 m
locomotory activity
1
ingestion
assimilation
growth
egg production
2
H14CO3-
incorporation in tissues
turnover rates
3
respiration
mucus
DOM
4
N2

Fig. 2. Diagrammatical representation of the experimental design, showing the rearing channel system (on top) and the chemostat culture for the experiments using algae (either ^{14}C labelled or non-labelled). Figures to the right refer to text. [1] shows the rearing channel systems. Some of the results are already reported in Streit (1981). [2] shows cultivation of algae in a chemostat and offering algal layers attached on millipore^{TM} filters to limpets within 100 ml wide-mouth Erlenmeyer flasks. Comparing ingestion, assimilation, growth of soft body and shell, and egg production allowed calculation of an energy budget for various sizes and temperatures (Streit, 1975a). [3] ^{14}C labelled algae allowed study of the allocation of organic material into individual organs and into eggs, and also estimation of organic carbon turnover rates in whole animals and in single organs. [4] Tracing the fate of ^{14}C released by the animal into the water allowed estimation of the relative importance of respiration, mucus secretion, and passive loss of soluble organic substances.

nally taken from population I, of a few thousand individuals, suitable for studies of body composition and physiology (Streit, 1978b, 1980) and of locomotory strategies (Streit, 1981; present study).

Studies of individual energy budgets were performed with freshly collected animals put individually into 100 ml wide-mouth Erlenmeyer flasks, provided with artificial periphyton. A 3-day acclimation time always preceeded measurements. The limpets were carefully placed with a long pincette on the algae-covered filter of individual chambers. There, they either stayed (eating or moving), or they crawled over filter and glass walls, only to return for eating. Limpets in a resting stage always migrated to the lower lateral parts of the glass wall and remained there motionless. Egg capsules, if any, were laid on the lower parts of the flask wall (which, for the limpets, represented the equivalent of the lower lateral areas of river stones). Capsules could easily be counted or removed with the help of a thin spatula for measuring total carbon and ^{14}C. The same flasks were used for feeding, assimilation, growth, and egg production studies and were slightly aerated with ca. 1 air bubble per 2 seconds. Experiments involving the study of ^{14}C uptake and allocation were carried out in a similar way, but some of the animals were transferred after the feeding period into chambers that were smaller in diameter, but higher and constructed so that nitrogen could be blown through from below. These chambers were used for the study of release of labelled CO_2, mucus, and dissolved organic material (DOM).

All bioenergetical data were based on carbon (labelled or non-labelled), and energy budgets were actually carbon budgets and carbon partitioning studies. In the following, we will first give a more detailed overview of the experimental design and then present the special analytical and preparational techniques.

A chemostat algal culture was the basis for feeding and growth experiments. The results presented in this paper are all based on studies with the diatom species, *Nitzschia actinastroides* (Lemm.) v. Goor. This alga was either used unlabelled (white arrows in Fig. 2.) or labelled (dark arrows). After the limpets were removed from the feeding chambers, all or part of the following parameters were measured:

Ingestion: The area grazed per day was measured planimetrically. Since the concentration of the algal layer (in terms of $\mu g\ C/mm^2$) was known, ingested energy could be expressed as μg C/day. Relative (or specific) ingestion rates were calculated by dividing the amount of μg C ingested per day by the carbon content of the soft body, assuming the following relationship (Streit, 1975a):

carbon of the soft body $= 6.64 \cdot AL^{2.66}$.
AL aperture length of the limpet
95% confidence limit of the exponent: 2.66 ± 0.08

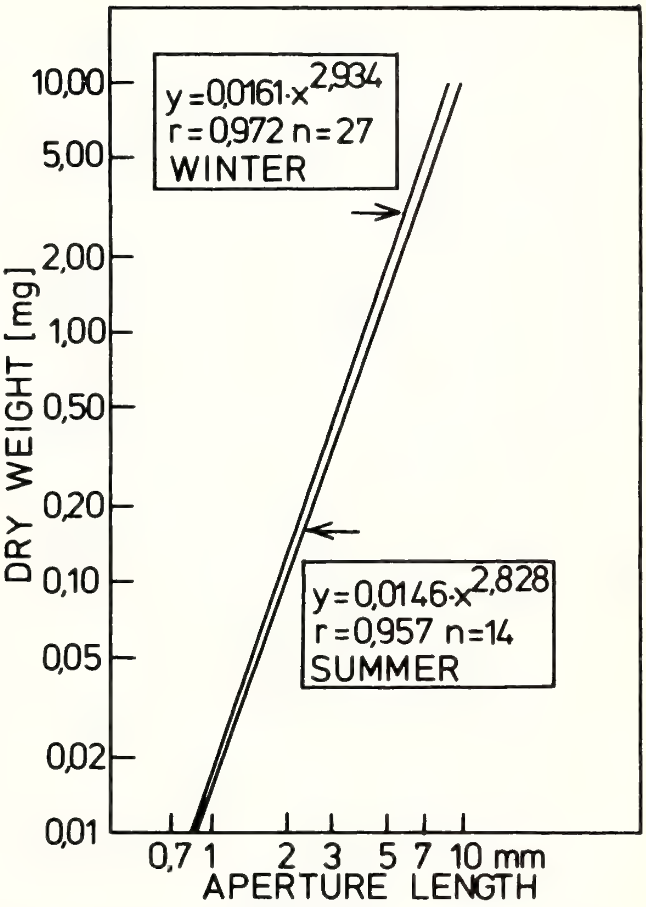

Fig. 3. Dry-weight of limpet soft-body vs. shell aperture length, plotted for winter and summer animals of population I. Winter animals (collected in January and February) are, on the average, 10.3% heavier than summer animals (collected in June). The difference is significant for the statistical mean ($P = 0.05$), though the confidence ranges overlap. The slopes of the regression lines are not significantly different.

The estimation of the carbon content according to relationship (1) is not free from a seasonally induced bias, since we know that the limpet dry-weight/AL relationship varies seasonally by about 10%, as shown in Fig. 3. We therefore assume a fluctuation in the limpet carbon content/AL relation also.

Assimilation efficiency was determined by calculating the difference of ingested food minus feces. For this purpose, the limpets and the millipore filter with its adhering remainder of the diatom layer were taken out of the vessels, and the fecal pellets, floating in the water, were collected by filtering the suspension over carbon-free diatomaceous earth. Then the latter was transferred into the C-H analyzer, where carbon content was measured. Values obtained by this method were corrected for an amount of 2.8% of secreted material within the feces (according to Calow and Fletcher, 1973).

Growth was determined in long-term experiments only and calculated from the increase in aperature length (AL) and a limpet-carbon / Al regression relationship. Due to the long-term character of these studies (1 to 3 months) and the constancy of environmental conditions maintained throughout the experiments, the error caused by a fluctuating limpet-carbon / AL relationship seems to be minor.

Egg production was measured in the same long-term experiments as the growth measurements. Limpets stuck egg capsules onto the glass wall of the flask, where capsules and eggs could easily be counted. Carbon content of capsules as a function of their egg numbers was presented in Streit (1975a) and used since for carbon estimations of capsules.

^{14}C release was measured by transferring individuals which had eaten within the last 3.5 hours, into empty chambers of a smaller size (filter diameter 20 mm). It was assumed that through this recent feeding process, the metabolic pool compartment of ^{14}C turnover (cf. Streit, 1975b; Lampert and Gabriel, 1984; etc.) contains roughly the same specific activity as the food does, and that respired $^{14}CO_2$ will initially come from this pool alone. After variable time periods, the limpets were again transferred into another empty chamber, and the same was repeated up to a maximum of 24 hours of total exposure. At the end of the experiment, the millipore™ filter was taken out of each chamber and analyzed for adhering mucus. A water sample was analyzed for total dissolved ^{14}C. After CO_2 was blown out from the remaining water by applying hydrochloric acid and N_2 to the system (Fig. 2, bottom), another water sample was taken. The difference between the first and second water sample represented respired carbon as $^{14}CO_2$, whereas the second water sample alone represented carbon that could not be evaporized by applying acid, and therefore essentially dissolved organic material (DOM), either leached from the limpet, or its fecal pellets (the latter produced in only minor quantities during non-feeding periods) or dissolved from mucus material. ^{14}C incorporated into the animal was measured also. During these experiments, the locomotory activities of the limpets were recorded regularly. Those individuals crawling repeatedly over the glass wall or even definitely abandoning the filter were not further used, since mucus adhering on the glass would have been too difficult to determine quantitatively.

TECHNIQUES

The carbon content of limpets was determined in shell-free individuals in a C-H analyzer, using O_2 for combustion of the organic material at 820°C. Soft-body parts could easily be separated from shell material by dipping the limpets for about a second into boiling water. The periostracum was separated from the remainder of the shell by dissolving the calcareous part in 1 M HCl. Carbon content of the algae was determined by filtering algal suspensions over carbon-free diatomaceous earth, transferring earth and algae together into small porcellain vessels of the oxidation chamber and ashing them together. Carbon determined in limpets and algae by this method represented rather total carbon than organic carbon. Developing CO_2 was trapped in NaOH and measured titrimetrically. Actual cell and carbon concentrations of algal suspensions during the experiments could instantaneously be estimated from photometric light extinction at 720 nm, using a calibration curve of extinction vs. carbon content of the respective algal species. An appropriate volume of the suspension, calculated from this estimation, was then filtered carefully over a 47 mm wide millipore™ filter with a pore size of 8μm. The area finally covered by algae on this filter was 1385 mm^2. Larger filters do not allow a homogeneous covering by algae. Algal cultures vary in their suitability for this method, since varying physiological states of the culture allow them to stick either easily on the filter, or only marginally. In the latter case, the algae would drop off after introducing the filters with the help of a long pincette into the water-filled feeding chambers. Cultures that were just at the verge of aging (due to exhausted nutrients and high density), were the easiest to handle. The maximum thickness that could be administered by this method, was 2 μg C/mm^2. The method failed usually with other algae than diatoms. The only way those species could be handled, was to mix them in a 1:1 ratio with diatoms (results about this latter aspect described in Streit, 1975a).

^{14}C was applied as $H^{14}CO_3$ to algal suspensions, which were incubated in a shaker overnight at ca. 8000 1x. Total carbon content and ^{14}C of the suspension was then measured, so that the specific activity of ingested algae was known. Specific activity changed only moderately within the first 24 hours of filter exposure, which allowed a suitable correction to be done (Streit, 1975b).

Protein determination of limpets was performed by the microbiuret method, described by Ithazaki and Gill (1964). Individual animals were dissolved in 5 ml 1 M NaOH at 80°C for 10 minutes. After centrifugation, 1 ml of the reagent was added to 2 ml of the supernatant. Photometric measurement was performed at 310 nm with and without $CuSO_4$ in the reagent to eliminate the color of the organic substances.

Carbohydrate was determined according to Dubois et al. (1956). Individual specimens were homogenized in 1 ml of water, then 1 ml of 5% phenol solution and 5 ml of the reagent were added. Photometric measurement was performed at 490 nm using glucose as a standard.

Lipid was determined by the sulphophosphovanillin method of Zöllner and Kirsch (1962). The usefulness of this method for lipid determination in various invertebrates has been shown by Barnes and Blackstock (1973). Individual specimens were dissolved in toto for 10 minutes in 2 ml of concentrated H_2SO_4 at 100 °C. Since the solution was free of suspended particles, neither filtration nor centrifugation was necessary. Aliquots of 0.1 or 0.2 ml were mixed with 2.5 ml of the reagent. Photometric determination was performed at 546 nm using a cholesterol standard.

RESULTS

Periphyton layers with diatoms were offered in the following concentrations according to a logarithmical scale: 2, 1, 0.5, 0.25, 0.125, 0.0625 μg C/mm^2. It was found that a lower and an upper threshold concentration existed for medium-sized limpets, beyond which, for two different reasons, algal patches are unsuitable as a food source (Fig. 4.). At concentrations of ca. 0.1 μg C/mm^2 and below, periphyton was never accepted. The limpets crawled over it as if the filter were free of any algal material. At higher levels (0.125 and 0.25 μg C/mm^2), the algal cover was accepted, but the amount ingested was lower than found at higher concentrations. Maximum ingestion was observed within a narrow window out of the concentration ranges found in natural periphyton layers, between ca. 0.3 and 2 μg C/mm^2.

The upper limit is attributable to mechanical problems in scraping too thick a layer from the surface by the radular mechanism. At 2.0 μg C/mm^2, the radula, due to its small dimensions, could no longer remove the whole food layer. The actual thickness of the periphyton layer itself could not be determined, but calculations show that a multiple layer of algae must be present at this concentration. The length of the radular teeth of a 5.5 mm limpet is 14.2 μm, whereas the lateral distance, measured between the tips of teeth, is 4.9 μm. *Nitzschia actinastroides* cells typically had lengths between 12 and 17 μm. The actual threshold concentration in the field may be slightly higher than 2 μg C/mm^2, as naturally adapted benthic algae on rocks adhere more tightly, but the difference from the experimental situation is probably small.

The physiological or behavioral basis of the lower end threshold limit is either the inability of detecting such a low concentration, or the active avoidance of grazing at this spot, since energy gains would be more than outweighed by metabolic costs. Whereas the first hypothesis (non-detection) is hard to prove, the second (cost higher than gains) could be tested by calculating the maximum theoretical ingestion possible at continuous grazing of varying concentrations, and relating this amount to known values of assimilation efficiency and total assimilation needs, as found in experiments supplying food at libitum.

In order to calculate maximum ingestion rates for different sizes and temperatures, the time needed for one single movement of rasping was measured with standard limpets of 4.5 mm AL. The speed of rasping is a strong function of temperature (Fig. 5a). Rasping is always combined with a slow oscillating movement of the head, so that each rasping area lies approximately adjacent to the preceeding one. At the end of each half-oscillation (at the right or left extreme) the limpet moves forward by a distance to graze just the next adjacent area. The number of rasping movements per half-oscillation is therefore fairly constant, and the area grazed is a function of limpet size, as shown in Figure 5b. The maximum area grazable by a standard limpet within 24 hours, if no break is taken, is an increasing function of temperature. The relationship to temperature is qualitatively the same as that found in Fig. 5a. The speed of the radular movements is not influenced measurably by algal thickness, so that the amount ingested per unit time—assuming no breaks—is a function of size, temperature, and food concentration (Fig.

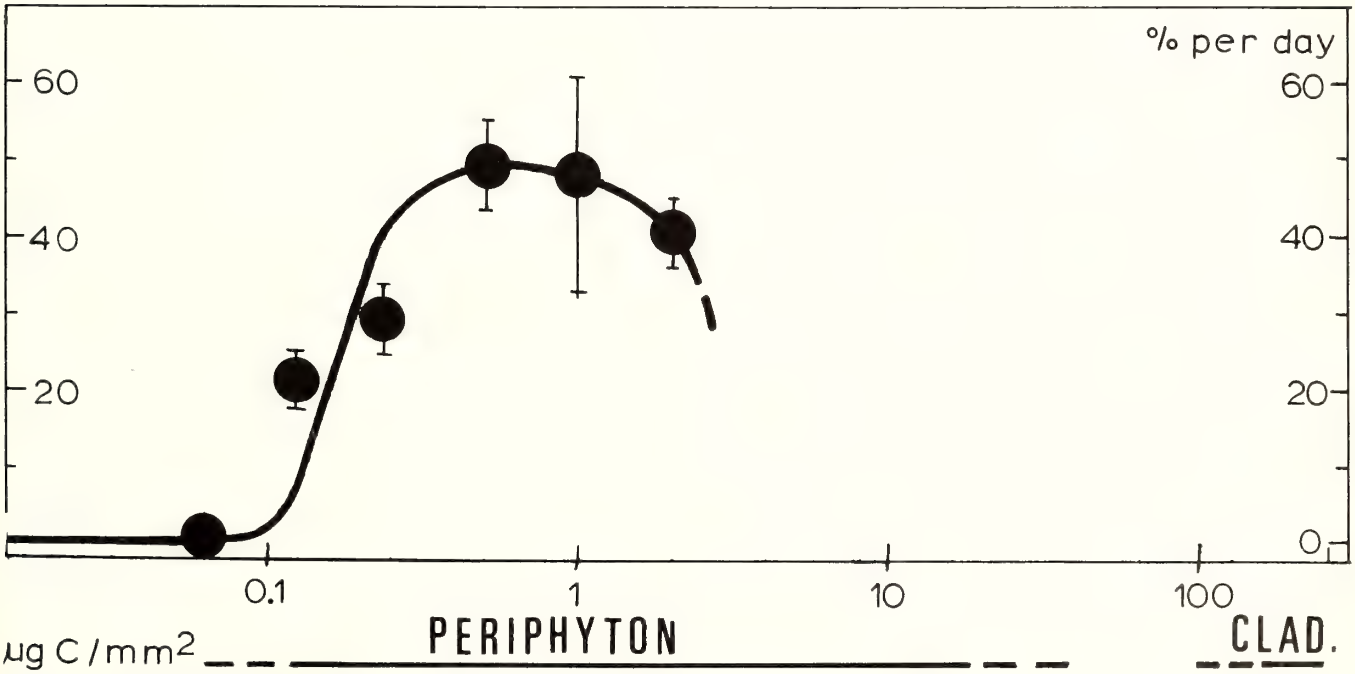

Fig. 4. Ingestion rate in terms of μg C/(μg C of limpet • day) at 16°C. Mean values and standard deviation. Adult limpets of an average aperture length of 5.5 mm were used. Below the frame are indicated the concentrations encountered in algal samples from the field (periphyton and Cladophoraceae, respectively).

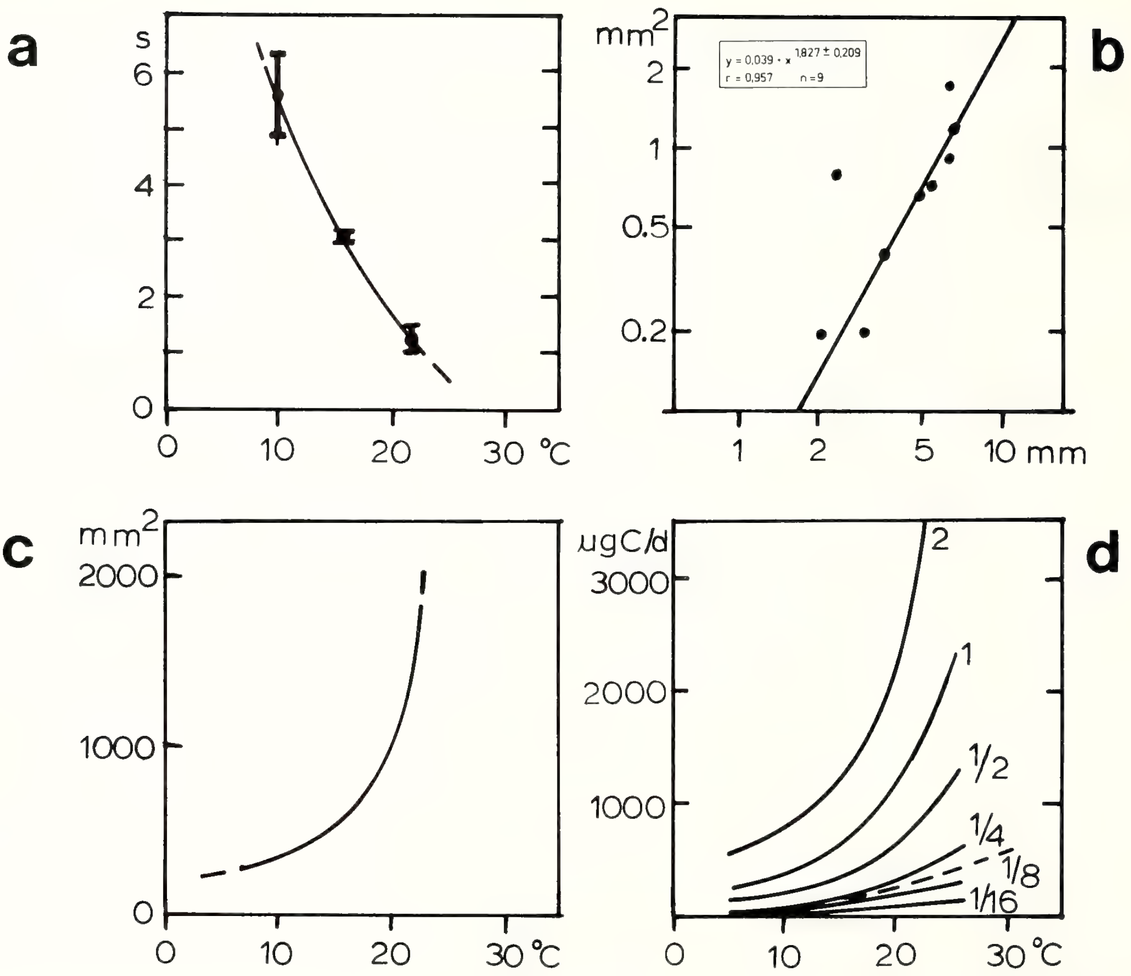

Fig. 5. a) Time in seconds (s) needed for one rasping movement of the radula of a standard limpet as a function of temperature (in °C). Mean values and standard deviation. b) Grazing area per half head oscillation (either from right to left or left to right) for different individuals, given as a function of aperture length (AL). This relationship is temperature-independent, but shows individual variability. c) Area per day that can be grazed by a standard limpet (4.5 mm) at different temperatures, assuming no breaks. d) Amount of carbon per day that can be grazed by a standard limpet (AL 4.5 mm) at different temperatures and concentrations (figures indicating µg C/mm²), assuming no breaks. Dashed line shows approximate minimum concentration for still optimal food supply.

5d.; curves are valid for a standard limpet). In addition, feeding rates vary seasonally. The values, if measured at equal temperatures, were highest in spring and lowest in fall (Streit, 1975a).

The outcome of this is that the number of hours per day which the limpet must spend on foraging, is a function of these parameters (size, temperature, algal concentration, season). However, the Q_{10} values of metabolic expenditures and radular scraping rates were approximately equal, as is shown in the following list, which gives Q_{10} values for the range of 12 to 22°C:

scraping speed:	3.52	(from Fig. 5a.)
ingestion in spring:	3.3	(Streit, 1975a: Fig. 21)
heart rate:	1.69	(for comparison; unpublished)

During the winter resting stage, scraping speed slows down, just as metabolism may slow down, and becomes also very irregular.

The similarity in the functional responses to temperature implies, that the time budget of a limpet is nearly independent of temperature in spring time. Time needed for feeding is thus reduced to a function of size, food concentration, and season.

It may be assumed that juveniles would be strongly restricted in encountering suitable grazing areas, if they were morphometrically totally similar to adult limpets. Their teeth would actually be too tiny to graze on the naturally uneven stone surfaces and collect large algal cells. The size of their teeth, however, is relatively larger than in adult limpets. Figure 6a. shows that the dimension of the whole radula in juveniles is actually at the maximum possible size. The radular sac (the generative zone of radula teeth) in freshly hatched animals stretches to the back end of the limpet. Starting with this enormous size, it decreases allometrically (Streit, 1975b) until it finally reaches a more typical size in larger animals. The two regression lines in Figure 6b. show the lengths (left) and lateral distances (right) of teeth, as found from microscopical measurements. These dimensions again grow allometrically with the limpet's age. The growth pattern keeps the crucial structural parts of the feeding mechanism within a limited variation of size ranges, probably corresponding to natural variations of periphyton layers and algal sizes, and also reducing the extremes between adults and juveniles.

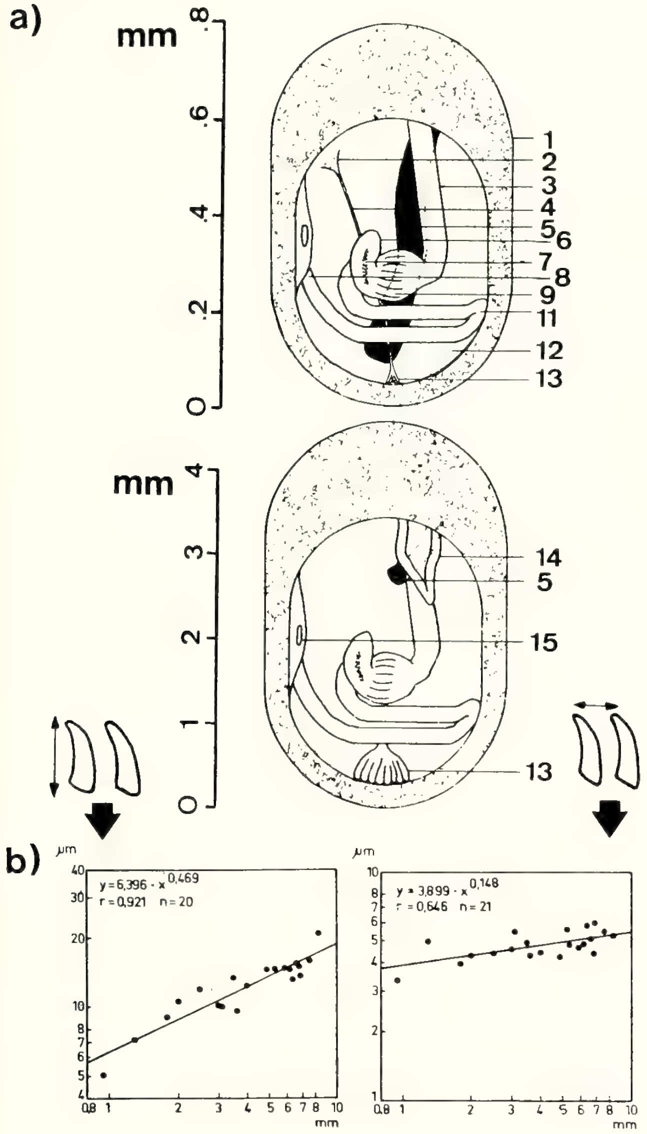

Fig. 6. a) Size of the radular sac as seen through the opened pallial complex, comparing juveniles (AL around 1 mm) and adults (AL 5mm). 1. edge of mantle. 2. formation site of female reproductive accessory organs. 3. esophagus. 4. hermaphroditic duct. 5. radula. 6. stomach caecum. 7. opening to midgut gland. 8. endgut and anus. 9. gizzard. 11. intestine (midgut). 12. pallial sac. 13. ovotestis. 14. foregut glands. 15. heart. b) The relationship between AL (on the x-axis) and longitudinal distance of the individual tooth rows is indicated in the left figure, between AL and latitudinal distance in the right figure. (Longitudinal distance equals approximately the length of individual teeth.)

Figure 7 shows the hours per day that are available for other activities than feeding, calculated for a limpet of 5.5 mm AL. The hours per day for other activities increase with increasing thickness of the algal layer and also with decreasing metabolic demands. A grazing period of 2–4 hours is about the minimum for active animals, whereas values of 24 hours are needed, if algal concentration is limiting. Critical concentrations are lower at reduced metabolism, as in summer, and for juveniles. This can be seen as adaptive, since winter animals and juveniles at stone lateral sides encounter naturally lower concentrations.

Applying the information obtained from Figures 5–7, we can interpret the values of Figure 4 as follows: The reason for lower ingestion rates at 0.125 and 0.25 μg C/mm^2, compared to maximum values, is caused by the limited food supply of the relatively slow uptake process possible with the radular movements. Though grazing nearly continuously, the energy gain is still below optimum. Temperature does not influence the characteristics of this curve markedly.

The variation in natural concentrations of algal layers is different in different river habitats. Figure 8 gives ranges of concentrations as found from a total of 60 patches, measured at different times of the year at site I through IV. Small areas of ca. 1 cm^2 were scratched from the rock surface with a blade. Areas that were obviously free of detectable algal layers, as are always found in rivers (especially at bottom sides of stones and around small pebbles) were omitted. Including those would result in bars extending close to 0 μg C/mm^2 at all four sites. Samples were taken from wherever limpets occurred, but bundles of Cladophoracean algae were excluded, since they are not eaten by the limpets. Areas of suitable concentrations are shown in dark grey; light grey shows concentrations only partially acceptable (other season, extreme sizes). Concentrations that are too high for grazing were found in three of the four localities. Too low concentrations, as mentioned above, may occur everywhere. Limpets must therefore move between patches and spend part of their time for locomotory activities due to foraging limitations alone. Besides suitable concentration ranges, food quality must also match their needs, as they avoid e.g., blue-green algae (Streit, 1975a). Also, local overgrazing on a stone will cause limpets to move further. Inherent behavior may additionally be responsible for further movements (see below).

Turning from considerations of intake to output aspects, the functional relationships between consumption, production, and production efficiency on the one hand, and temperature and size on the other were determined. Consumption rate increases with the temperature up to a maximum value of 25°C, which at the same time is also the upper temperature limit for long-term survival of *Ancylus fluviatilis* individuals (Fig. 9a.). Maximum production was found at

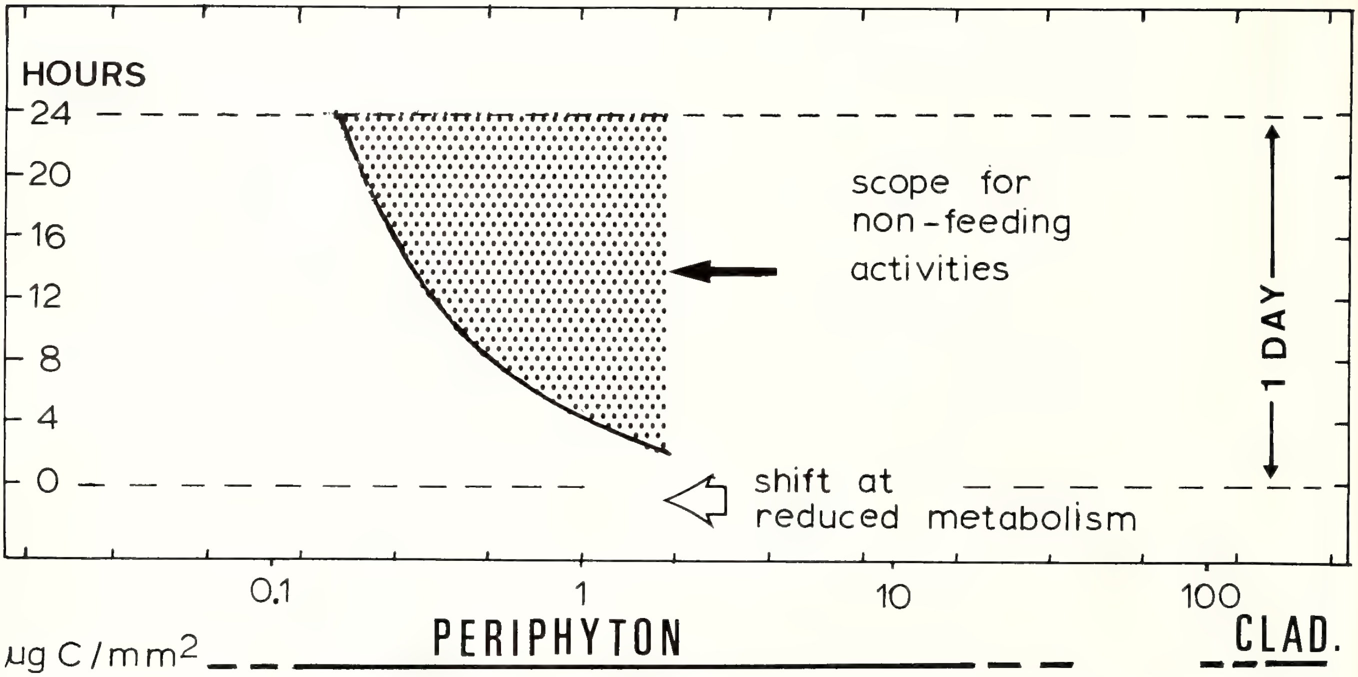

Fig. 7. Daily time budget for a 5.5 mm limpet, using ingestion rates as determined in optimum concentration ranges. The dotted area indicates the number of hours per day that can be used for other activities than feeding, plotted as a function of algal concentrations. In times of reduced metabolic activities (i.e., summer through winter), the area would shift towards left.

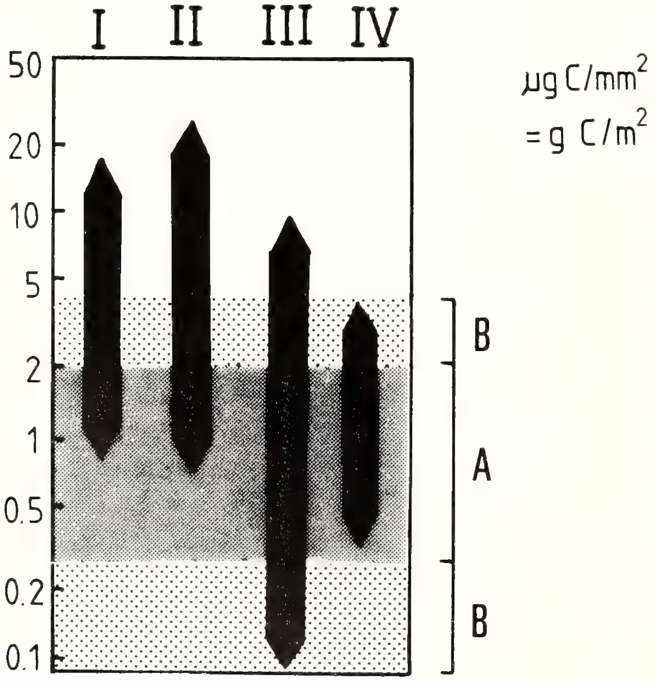

Fig. 8. Concentration ranges of algal patches in habitats I-IV, as found by scratching layers with a blade and analyzing them in a C-H analyzer. Concentration areas that are considered to be suitable for most individuals, according to the results in Fig. 4, are underlaid in dark gray (A), those perhaps partially suitable in light gray (B).

around 19°C. However, at this temperature, production efficiency (i.e., production/assimilation ratio) is no longer at its maximum. The highest efficiency is found at 13°C. Given an unlimited food supply and no competition, the highest specific production rate and population density of a limpet population should occur around 19°C. Under food competitive pressure, efficiency optimization might be more important, and 13°C would reflect a strong competitive temperature zone for *Ancylus fluviatilis*. This latter is indeed the temperature that is typical in spring for many habitats where this limpet occurs.

Carbon partitioning between growth and egg production is also a function of temperature as in Fig. 9b. The percentage allocated for eggs steadily increases from 7 to 13°C, but then remains about constant up to the lethal temperature. At increasing temperature, maximum production efficiency and maximum allocation of energy for reproduction coincide at 13°C. As a result, a rather explosive egg production period may be observable in spring, when water temperature rises.

A summarizing set of data, containing aspects of input and output, as considered so far, is given in Table 2. Energy budget values are presented for different temperatures and sizes, calculated from experimental data, assuming a food concentration of 1 µg C/mm^2. Temperatures of 10°C and 19°C are considered for three sizes of individuals: freshly hatched juveniles (10 µg C, corresponding to 1.2 mm), medium sized young limpets (100 µg C, 2.8 mm) and large adult ones (100 µg C, 6.6 mm). The values are all taken from

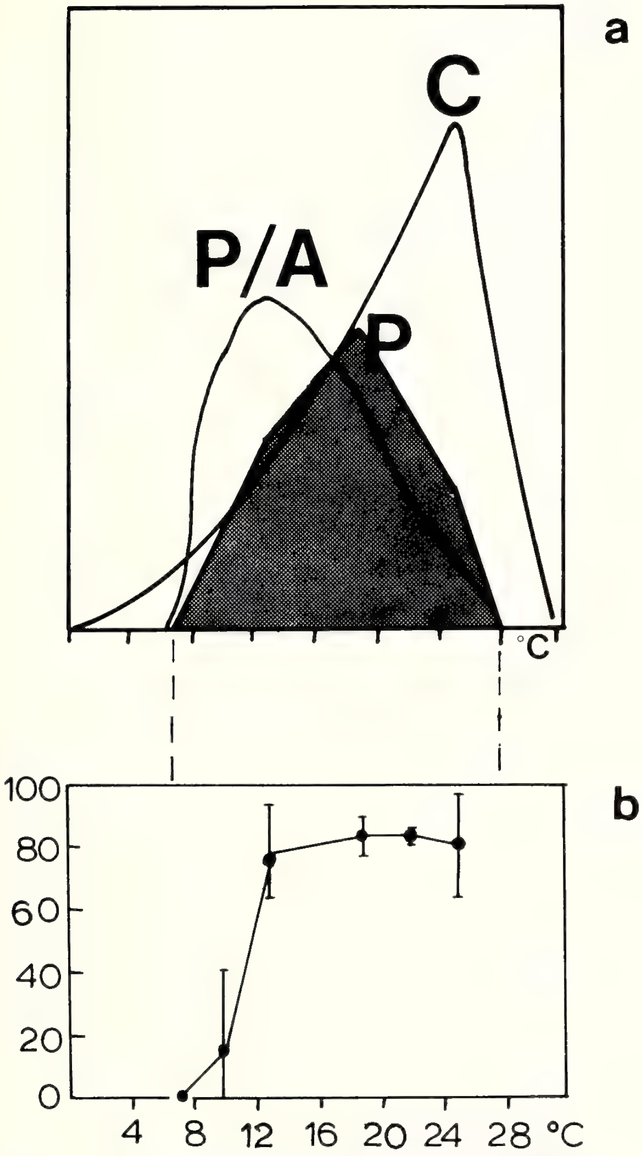

Fig. 9. a) Consumption (C), net production (P; growth and egg production), and net growth efficiency (P/A; production/assimilation) as a function of temperature. Scales for the three plots differ. b) Allocation of production energy into eggs as a function of temperature. The difference to 100% is growth production. Values are for adult limpets.

Table 2. Energy budgets of population I limpets. Values in 2–5 represent relative rates (μg C/[μg limpet C · day]) as determined from experimental measurements, calculated for freshly hatched (10μg C), young-to-subadult (100 μg C) and large adult (1000 μg C) individuals. Ingestion and assimilation rates were assumed to be size independent as found in spring time maximum activity. (This is an extended [and in 1 figure corrected] table from Streit 1975b, p. 21).

10°C	10 μg C	100 μg C	1000 μg C
1. limpet size as tissue carbon content	.166	.166	.166
2. Ingestion	.087	.087	.087
3. Assimilation	.069	.033	.010
4. Soft body Production growth egg capsules	.069	.033	.0085
5. Periostracum production	.000	.000	.0015
6. Production/Assimilation efficiency	.004	.002	.0006
	83.9%	40.2%	12.2%

19°C	10 μg C	100 μg C	1000 μg C
1. limpet size as tissue carbon content	.505	.505	.505
2. Ingestion	.327	.327	.327
3. Assimilation	.173	.065	.025
4. Soft Body Production growth egg capsules	.173	.065	.005
5. Periostracum production	.000	.000	.001
6. Production/Assimilation efficiency	.011	.004	.001
	56.3%	21.1%	8.0%

regression lines of experimental data vs. temperature and size variation. Allocation of energy into eggs (vs. growth) is a function of size and temperature; the percent use of energy for the periostracum, however, is independent of size and temperature (although dependent on the actual state of activity, cf. Streit, 1978a). Production efficiency (P/A) is higher at 10°C than at 19°C, and juveniles are better energy converters than larger limpets. P/A for young limpets at 10°C is as high as 83.9%; P/A for large limpets at 19°C is only 8.0%. Since the standard metabolism, as measured from respiration values, usually declines rather than increases during growth, the lower efficiency in larger limpets must be due to an increase in non-productive activities, such as moving and resting.

Freshwater limpets encounter nonrandom, clumped dispersion patterns of their food items on the river bottom and have adopted a random walk behavior with additional behavioral mechanisms to increase the chance of finding suitable patches. In areas of suitable food concentration, they tend to stay for a longer period than in other areas, but nonthe-less leave the place again after some time. Thus the foraging rules of this species seem to be a combination of "area restricted searching" and "giving up time" strategy (Streit, 1981). This behavior is, however, seasonably variable (Streit, unpublished). Since the distances to cross between suitable patches may sometimes be quite long, we asked what the effect of extended non-feeding periods on the energy allocation pattern of limpets would be.

Twenty animals were kept at 19°C, starting in May. After 24 days, they were deprived of food and kept for another 16 days. Their carbon content was measured at the beginning of the starvation period and after 4 days, 8 days, 12 days, and 16 days. During the first eight days, the carbon content of the limpets was reduced by 4.2% each day on the average. This is only slightly higher than estimated for respiration of *A. fluviatilis* at the same temperature (3.8%), using the data presented in Berg et al. (1958), the surplus being probably attributable to secreted material. The daily decrease in carbon content from the 8th to the 16th day was only around 1.8%. A carbon content of about 50% of the original value, as reached around the 16th day, turned out to be about the lethal limit.

Egg capsules were deposited continuously until the end of the experiments. However, whereas one capsule per limpet was laid every other day in the beginning of the starvation experiment, the rate slowed down to one capsule every fourth day by the end of the experiment. The average carbon content per egg was not significantly different from non-starving limpets.

These results suggest that the limpets, once activated endogenously, stay in an active stage (in a "geared-up" activity of metabolism), even when deprived of food, until they finally starve to death.

Two questions immediately arise in connection with energy storage capacity: How fast are different pools of fuel reserve used up during starvation periods, and what effect will the restoring of food sources have on reproduction rates?

Figure 10 shows the course of proteins, lipids, and carbohydrates in limpets, starving for 12 days at 19°C. Whereas protein is reduced at approximately equal rates over the whole period, lipids are obviously used first for energy consumption (between day 0 and 2), and carbohydrates secondly (day 2–4). Only after this period will the body reduce its constituents at approximately equal percentages.

Further studies showed that the initial lipid decrease occurs primarily in the midgut gland, which is the major storage organ for lipids and provides immediate energy needs. Carbohydrate is mobilized from all over the animal (Streit, 1978b). A shortage of food for a couple days seems insignificant for the overall metabolism even under high sum-

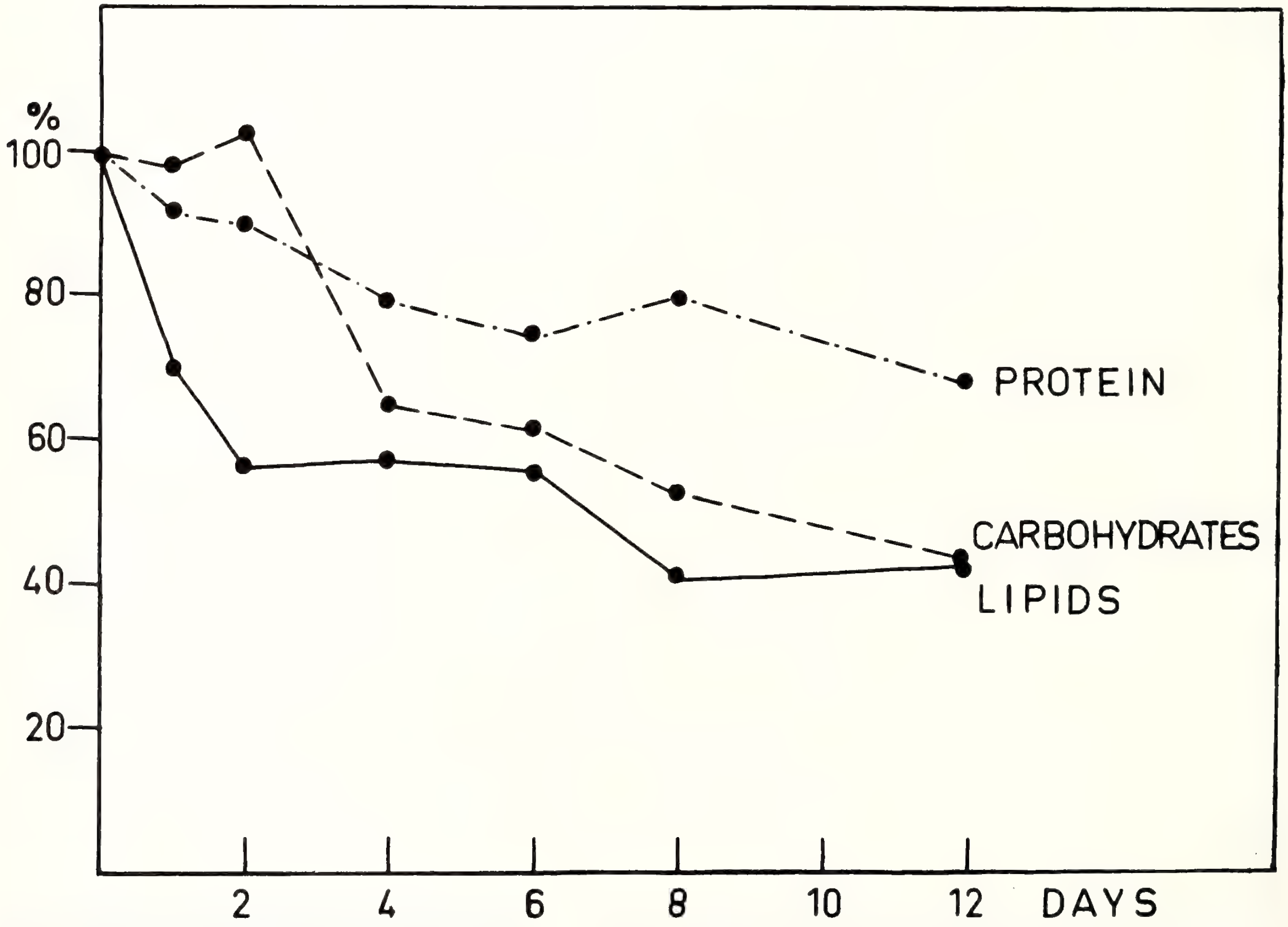

Fig. 10. Protein, carbohydrate, and lipid content in limpets (AL = 4 mm), deprived of food, measured at 19°C. Lipid reserve is diminished first (day 0–2), followed by carbohydrates (day 2–4).

mer temperatures. However, it is a stress situation for the limpets and causes a reduced egg depositing rate.

Extended periods of starvation resulted in a lower absolute carbon allocation into egg capsules, which means, since eggs do not become smaller in size, the number of eggs per capsule diminishes. The following experiment was carried out to find out, whether a new feeding period, succeeding a starvation period, would finally result in a fill-up of the animals' deprived storage pools, and then let the animals behave as if there had always been enough food.

After starvation times of 3, 6, and 9 days, limpets were fed again at libitum. Immediately after refeeding, egg capsules were again laid regularly, but at reduced egg numbers. The average number of eggs remained constant in the course of each experiment, without any declining or increasing tendency. After a starvation period of 6 days, some of the subsequently deposited egg capsules contained just 2 eggs. After 9 days, even capsules containing only 1 egg were observed. The average allocation ratio of tissue growth vs. egg production in these experiments was not significantly different from the ratio found in the other experiments (78.5% vs. 81.2% into reproduction, and 21.5% vs. 18.8% into soft-body tissue growth). Therefore, no compensation either into enhanced tissue growth allocation or into reproduction was observable after a starvation period.

The locomotory activities include horizontal and vertical components and reflect varying states of activity. Preferred sites of occurrence on stones vary with varying temperatures. A 70 day temperature program was therefore run in one of the channels, where limpets from population I were kept. The percentages of limpets on top, bottoms, and sides of stones are shown in Figure 11a. together with the temperature curve. Animals encountered on top of stones were also the most actively feeding (Streit, 1981) and increased in number at higher temperatures at the cost of those staying on bottom or lateral sides (Fig. 11b). Relating river temperature variation to preferred occurrences in two field populations showed similar results, although switching from bottom to top sides occurred at different temperatures. Population I individuals still resembled the functional response of channel system limpets more than population IV individuals did (Fig. 11c).

Time budgets of individual limpets turned out to be highly unpredictable, although the population on a whole exhibited predictable functional relationships. Experimental time budgets for two individuals kept at 7°C, and for one kept at 16°C, are shown in Figure 12a. Recordings were made every hour. The occurrence of resting, movement, or feeding was noted. If feeding occurred, ingestion rate per hour in percent of the individual biomass (specific, or relative, ingestion rate) was calculated. The animal in the upper-most figure was in a fairly active physiological state and consumed between about 0.2 and 3% of the body weight in 9 of 24 hourly recordings. The animal in the middle figure was rather inactive and remained motionless for most of the period. The bottom animal ate amounts of 1–8.5% per hour during 13 hourly recordings. The maximum ingestion rates per hour in any of the three limpets come close to the upper mechanical limit of uptake, determined by the inherent rasping speed (values are higher at 16°C than at 7°C, since rasping is faster).

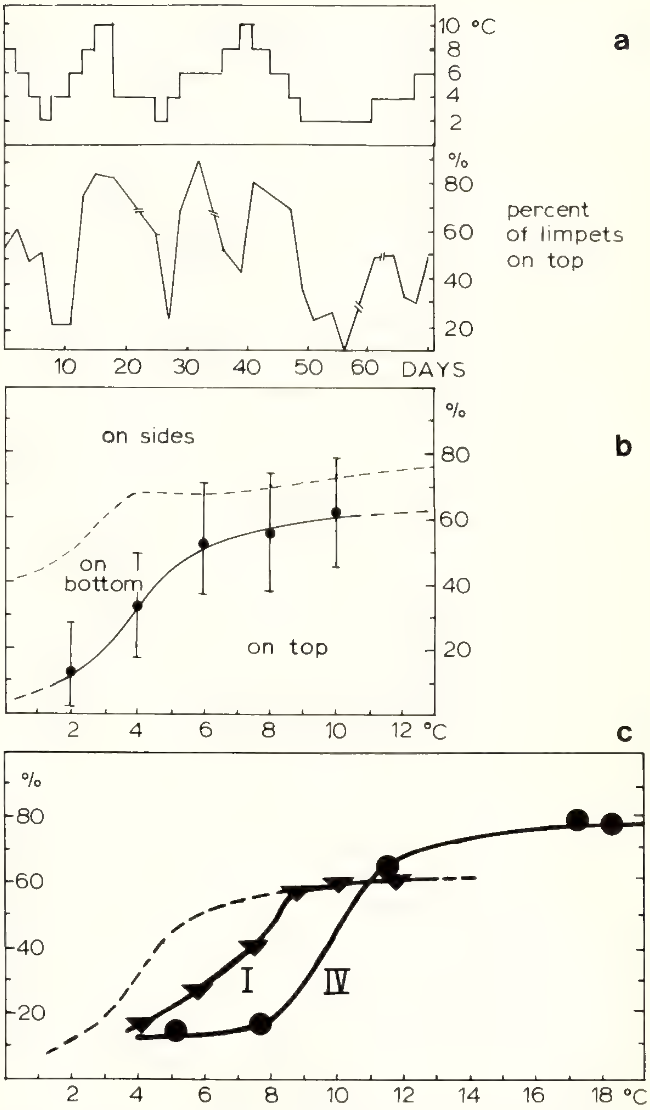

Fig. 11. Relationship between preferred location in a channel section and ambient temperature in a 70 day experiment: a) Temperature program (upper figure), that was run in one of the rearing channels (Fig. 2), and percent limpets found on top of stones (lower figure). At line interruption times, some new individuals were added into the experimental section to replace those crawling on glass walls. b) Continuous line (with mean values and standard deviations) gives percent limpets on top of stones as a function of temperature. The area between this line and the dashed line shows percent of limpets on bottom sides of stones. Between dashed line curve and the top horizontal the percentage of limpets on the lateral areas of stones is indicated. c) Comparison of the above curve (% limpets on top of stones, shown again in dashed line) with natural percentage of animals on top from population I and IV.

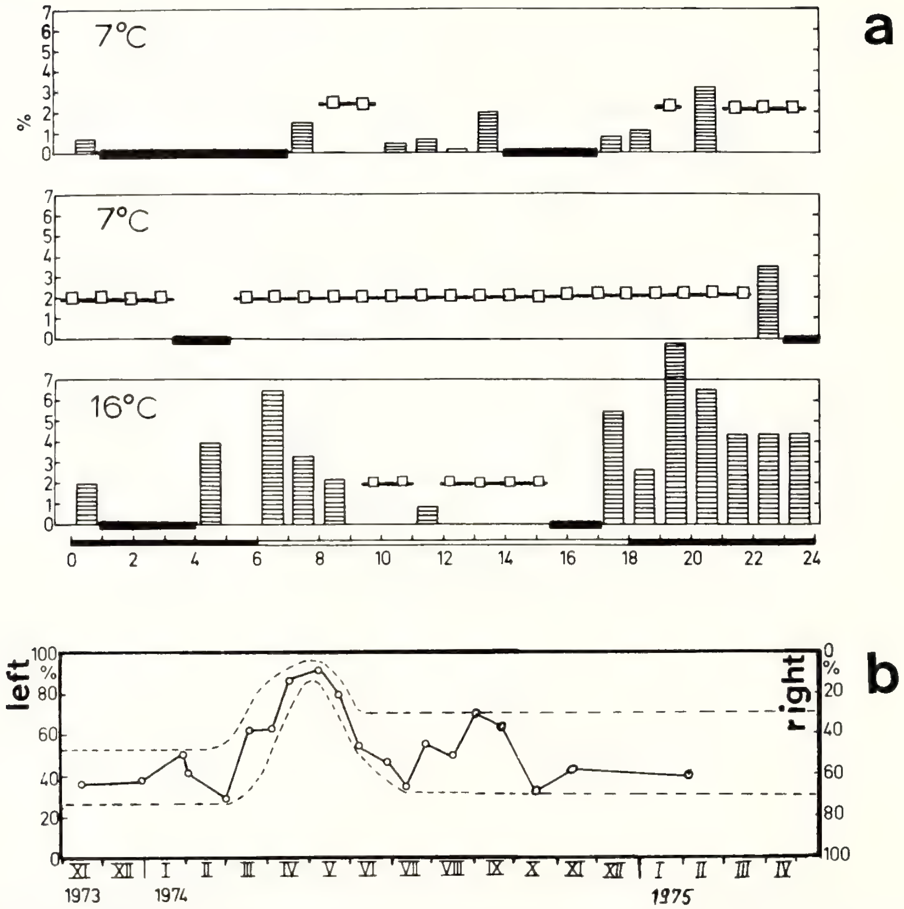

Fig. 12. a) Three examples of daily time budgets at 7°C and 16°C, as found in experiments with 0.5 μg C/mm². Horizontal black bars indicate resting times. Vertical bars show relative amount of ingestion per hour. Remainder of time (shown by squares) was used for locomotory activities in the glass vessels. b) Distribution of population I over the width of the river area (2 m wide) at different times of the year. During springtime, at maximum development of diatoms on the left side, there was an overall migration of the population in this direction, which later in the season diluted again.

The "area restricted searching" and "giving up time strategy" of these limpets (see above) should automatically lead to local aggregations at suitable microenvironments. Such distribution could be observed directly in population I field studies. During springtime both, periphyton growth and maximum density of the limpets was highest in the shallow part of the river. The near-random rest-and-move behavior with extensive crawling periods over unsuitable environments enables the animals to locate suitable grazing sites. The result corresponded to an overall orientated migration of the population by about 1 meter (Fig. 12b).

Locomotory activities are the major reason for high energy losses not only through respiration, but also mucus secretion, and DOM release. DOM can either originate directly from body-leaching or from the secreted mucus.

An estimation of respiration rate, mucus, and DOM loss was possible by feeding ^{14}C labelled algae for a time period enough to fill up short-term turnover compartments in the limpet metabolism, and tracing the release of ^{14}C into the environment. A direct measurement of ^{14}C release by the animals during feeding is not possible because of the interference of the released material with the metabolism of the algal layer. It can, however, be assumed that organic material entering the body will first be processed through a metabolic pool with a high turnover rate and thus, for a limited period, be released as CO_2 with about the same specific activity as assimilated (Streit, 1975b; Lampert and Gabriel, 1984). We here assume that also mucus and DOM originate directly from the metabolic pool. After cessation of feeding, a shift towards use of other metabolic C-sources will eventually cause a decline in a specific activity of released carbon material.

The amount of ^{14}C recovered as CO_2 (Fig. 13; figures expressed as a percentage of total assimilated ^{14}C) increased most rapidly during the first 40 minutes after the transfer. This is the period assumed to represent the release of $^{14}C/^{12}C$ with the same specific activity as when assimilated and ingested. From the knowledge of the specific activity of the algae, respired carbon was calculated as 2.4% per day at 19°C.

Labelled carbon allocated for mucus secretion was lower, that for DOM release higher, than for respiration, as can be qualitatively seen from Fig. 13. The total amount of nonproductive carbon loss is therefore around 8–10% per day (related on the weight of the limpet, at 16–19°C), or around 50% of the assimilated carbon (Detailed studies in progress).

The "instantaneous" production efficiency, as found from studies of incorporation values vs. losses, is around 50% in adult limpets, even at 19°C, and thereby comparable to juvenile long-term production efficiency (cf. Table 2). The combination of rest and movement with feeding periods in older limpets gradually lowers their production efficiency considerably.

A preliminary summarizing result of the energy budget of adult *Ancylus fluviatilis* is finally presented in Table 3. The figures are based on previous studies (Streit, 1975a,b; 1978a) as well as those presented in this paper. The importance of mucus and DOM in the energy budget is well demonstrated.

Table 3. Preliminary "complete" energy budget of an adult *Ancylus fluviatilis*, calculated for 13°C and a shell aperture length of 5.5 mm. Calculations based on experiments carried out with population I limpets. Figures in the left column expressed in [μg C/(μg limpet carbon · day)] × 100, in the right column given in percent of carbon ingested.

	percentage in relative terms	percent of ingestion
1. ingestion	26.2 %	100 %
2. assimilation	13.4 %	51 %
3. feces	12.8 %	49 %
4. growth: soft body	0.28%	1.1%
periostracum	0.02%	0.1%
5. egg production	1.23%	4.7%
6. total tissue production (4. + 5.)	1.53%	5.9%
7. mucus	2.7 %	10 %
8. dissolved organic material	3.7 %	14.0%
9. secreted material in feces	0.7 %	2.8%
10. total organic losses (7. – 9.)	7.1 %	26.8%
11. total production (6. + 10.)	8.6 %	32.7%
12. respiration	3.8 %	14 %
13. total production + respiration	12.4 %	47 %
14. unidentified error of individual estimates (2. minus 13.)	1.0 %	4 %

DISCUSSION

Several bioenergetic features have been considered unusual in *Ancylus fluviatilis*, among which is the low net-growth rate, especially in large individuals (Streit, 1975a, b). A low growth rate of an animal species can be the consequence of a quantitatively or qualitatively poor food supply or of high metabolic energy costs, ultimately for survival reasons. It can also be the consequence of a predation pressure so that growth is directly limited by avoidance and nonfeeding. In *A. fluviatilis*, high predation pressure is only occasionally found, so that the unpredictability of adequate substrates and food patches within the running water system may have selected for high metabolic costs due to locomotory activities.

Populations may differ, possible genetically, in the percentage of time spent in different activities, and thereby also in overall efficiencies. Black Forest populations (at an altitude of 920 m above sea level) are totally inactive in winter months and individuals may be found at exactly the same locality (at the bottom side of a single stone) for two months or so (Schwenk and Schwoerbel, 1973). In rivers of only moderately cool winter temperatures, they remain more active. The critical temperature that determines whether the limpet's metabolism is either activated or resting was originally assumed to be around 6°C (Schwenk and Schwoerbel, 1973). Populations may, however, exhibit different functional temperature responses, so that the switch may occur anywhere between 5°C and 10°C (cf. Fig. 11, bottom). They may also show different tactics such as an obligatory resting phase with strongly reduced metabolism, as in Black Forest populations, or a slightly reduced metabolism only, as in population I. The field data presented in Table 1 indicate that egg output in IV, compared to energy units assimilated, is higher

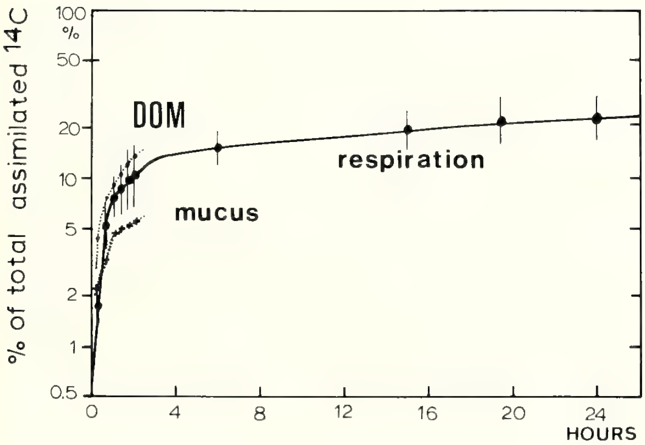

Fig. 13. Eliminated ^{14}C from animals which have eaten labelled food within the last 3.5 hours before the experiment. The sum of ^{14}C from limpet, respiration, DOM, and mucus is set to 100% and assumed to represent assimilation. Only the initial increase in ^{14}C is used for interpretation here. Solid line and bars: respired ^{14}C and standard deviation (over 3 experiments with 3 limpets each). Upper dotted line: recovered DOM. Lower dotted line: mucus adhering on filter.

than in I, so energy conversion is more efficient. Populations I–III, however, seem to have higher mobility components, and working in that river often results in getting limpets attached on hands or shoes. This difference may be related to variable fitness demands.

Number of egg capsules deposited, as reported in literature, was 14 in Lamberet's (1966) population, whereas Russell Hunter (1953) estimated 12 capsules per individual on an average and Geldiay (1956) between 10 and 20 (rather to the lower figure). Maximum numbers of total eggs reported are 57 (Lamberet, 1966), whereas mean values of 50 are reported by Geldiay (1956) and 46 by Russell Hunter (1953). Very low figures were reported by Bondesen (1950; 4–7 capsules per adult, with 2.6 eggs each on an average; largest number of eggs: 41). It may be assumed, however, that his figures reflect some adverse experimental conditions. Our own figures (66–113 eggs per individual; Table 1; Streit, 1976c) are comparatively high. Although different counting methods were involved, we assume the different egg numbers reported to be evidence for either environmentally or genetically induced variable allocation patterns.

Optimum energy allocation for survival and dispersal of benthic grazing invertebrate populations is dependent on the strategy adopted by the species under consideration. Short-lived adaptable small grazers which quickly approach the local carrying capacity, may have high net-growth rates and never spend much energy on dispersal or predator avoidance, as e.g., in the naidid worm *Stylaria lacustris* (Streit, 1978c). If their populations are threatened by local overgrazing, they ultimately undergo sexual reproduction and overwinter in a resting stage. By contrast, herbivorous insect larvae (Ecdyuronidae, etc.) may often recolonize locally extinct patches by means of larval drifting or adult flight dispersal. Both strategies are impossible for limpets. They therefore have developed a behavioral and allocational system that can prevent an overshooting of population density at local spots.

Reproductive effort (expressed in reproductive biomass as a percentage of growth) has been estimated for other freshwater snails (Aldridge, 1982; Browne and Russell-Hunter 1978, and others). Although the methods used differ, reported values seem on the average to be lower than 81.2% of net production directed toward eggs, as found here between 13 and 25°C.

High losses of soluble organic compounds, as detected in released DOM values, may be the result of a high permeability of the limpet's epithelium for many inorganic and organic compounds. The half life in exchange of labelled water molecules between the environment and the body compartment is about 2.5 minutes (Streit, 1980, 1982). The time needed for a pesticide entering the limpet's body to equal the environmental concentration is about 18 minutes with the moderately lipophilic herbicide atrazine (Gunkel and Streit, 1980), and is similar with the stronger lipophilic insectcide lindane (Streit, 1979).

The reverse of the loss of soluble organic substance, the selective uptake of DOM from water, was not demonstrable and therefore cannot be considered to exceed passive diffusive exchanges and be a source of energy gain (Streit, unpublished, using labelled algal exudates).

Preliminary data on energy costs for locomotion in *Ancylus fluviatilis*, as calculated from Fig. 13 data and other information, made it possible to estimate the cost of movement of this limpet per unit weight and length. The result is plotted in Fig. 14, which gives energetic costs for various other types of locomotion taken from Schmidt-Nielsen (1975) and Pianka (1983). Calculations were made with limpets of 4 mm AL, a temperature of 16°C, and a crawling speed of 1 limpet unit length per 30 seconds, which can be considered a relatively high speed on smooth surfaces (Schwenk and Schwoerbel, 1973). The costs of movement are extremely high in limpets and comparable only to those of other snails. Selection pressure for spending as little energy as possible into locomotion, is possibly quite high, especially under food limitation or competition.

Locomotory activities enable the limpets to find new food patches, and even to include long resting phases in sheltered areas of stones to slow down population growth, and also to cross between adjacent stones. Locomotion may also be a key factor allowing long-distance transport through random attachment to birds and beetles, which occasionally has been reported in literature (e.g., Buttner, 1953). Genotypes of highly mobile populations—and therefore automatically poor energy converters—may have a higher recolonization potential for transient water systems, such as for areas only accessible since the last glaciation. Long-term stable systems by contrast may enhance the advantage of high-efficiency competitors. From our data in population IV it appears, that even within areas recolonized since the end of the pleistocene, competition in the meantime has resulted in high efficiency populations. High adaptation rates to local

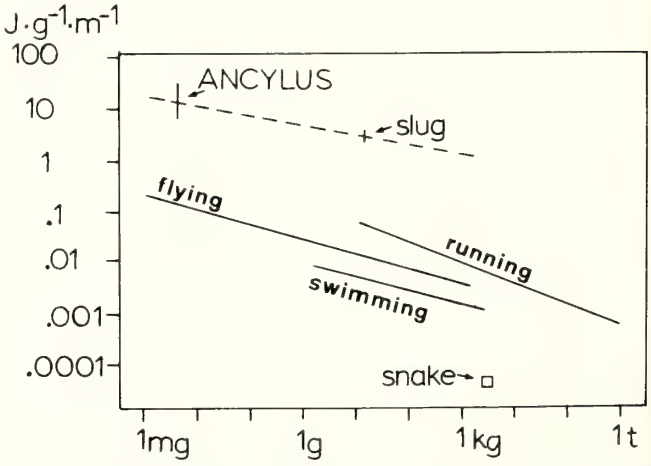

Fig. 14. Comparison of energetic costs (in terms of $J \cdot g^{-1} \cdot m^{-1}$) of moving a unit of body weight 1 meter for different modes of locomotion in multicellular animals of varying fresh weights. According to Schmidt-Nielsen (1975), Pianka (1983), and own results.

conditions, such as temperature response, have been reported to occur even within a few dozen generations in basommatophoran snails (for a recent review see McMahon, 1983).

One general and important conclusion that can be drawn from a simple ecological optimization model is that the switch from growth and locomotory activities to reproduction during ontogenesis should occur as soon as the mortality rate equals or exceeds the production rate (Ziolko and Kozlowski, 1983). From population density measurements of *Ancylus* and the leech *Glossiphonia complanata* (the major predator of *Ancylus* in populations I–III, but not found in IV) predation pressures can be assumed to fluctuate from year to year, and the same is true for mortality rates due to abiotic reasons (unpublished observations). It is unknown whether populations have been selected for average local situations or whether selection varies from year to year. A striking switch in behavior and energy allocation is observed in spring from high-energy expenditure on locomotion to high rates of feeding and egg production. It could be that this switch is not very fixed without predation, but that it could adapt to optimum timing under the influence of high mortality over a few generations. Model studies on this aspect are in progress.

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SEASONAL PATTERNS OF CARBON AND NITROGEN PARTITIONING IN THE FRESHWATER PROSOBRANCH *LEPTOXIS CARINATA*

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ABSTRACT

Regular sampling from three populations of the freshwater prosobranch snail *Leptoxis carinata,* established its life-cycle as biennial and semelparous, with patterns of oxygen uptake, nitrogenous excretion, and growth reflecting the effects of age, season, life-cycle events, trophic input, and sexuality. Assimilation rates for an average snail ranged from 39 to 49 mg C/lifespan for protein and 24 to 51 mg C/lifespan for nonprotein. Net growth efficiencies ranged from 20 to 26% for protein carbon per lifespan and 1 to 5% for nonprotein carbon. In all cases males show lower growth efficiencies than females. Lifespan seasonal patterns of carbon acquisition and expenditure are similar in the three populations. Nonprotein carbon is acquired slowly and relatively continuously. In contrast, most of the protein carbon is acquired during a snail's second summer. Nonprotein carbon accounts for 50 to 60% of lifespan metabolic expenditures and contributes more during the spring and early summer. Protein carbon's contribution to contemporaneous expenditures is highest in the summer.

Most earlier work on ecological bioenergetics of aquatic poikilotherms has involved measuring oxygen uptake rates of organisms under various laboratory conditions, so that rates of catabolic metabolism under field conditions could be estimated (Berg, 1952; Teal, 1957; Mann, 1965; Burky, 1971; Mattice, 1972; McMahon, 1973). More recently, the contemporaneous assessment of nitrogen excretion and oxygen uptake rates has permitted the assessment of the relative utilization of protein and nonprotein carbon sources reflecting internal shifts in catabolic partioning patterns (Bayne 1973 a,b; Widdows 1978; Russell-Hunter et al., 1983). These efforts complement data available on the anabolic patterns of resource partitioning (Russell-Hunter, 1970; Apley, 1970; McMahon, 1975; Hunter, 1975; Browne, 1978) and provide a more integrated picture of resource partitioning and, hence, a more complete view of the physiological limitations which shape life-history traits. Earlier work on oxygen uptake and nitrogenous excretion has been mostly directed at the effects of temperature (Segal, 1961; McMahon, 1973), oxygen tension (Berg, 1952; McMahon and Russell-Hunter, 1977) and salinity (Gilchrist, 1958; Kinne, 1966). Less work, however, has been done on the effects of catabolic pattern of age and sex or of trophic input, which contribute to bioenergetic variation in natural populations of aquatic invertebrates (Russell-Hunter, 1964; 1978). Evaluation of the patterns of oxygen uptake and nitrogen excretion along with concurrent estimates of growth during the life cycle is important in discerning partitioning of available resources (Bayne and Widdows, 1978). Such evaluation is important in determining to what extent intrinsic factors (such as age and sex) and extrinsic factors (such as season and food quality) affect efficiencies and realized growth rates (Russell-Hunter, 1964; 1978; Widdows, 1978; Russell-Hunter and Buckley, 1983). As potential reproductive output in most poikilotherms is a positive function of size, growth (within environmental limits) becomes an important component of fitness. Hence the factors influencing growth and partitioning are of primary importance in studying intraspecific variation to allow discussion of the evolution of life-cycle patterns (Russell-Hunter, 1964; 1978; Calow, 1977). Aside from this academic interest in partitioning studies, there is an increasing applied interest in using various numerical indices of bioenergetic partitioning to assess degrees of environmental "stress" on individuals and populations of aquatic poikilotherms (Bayne, 1973b; Widdows, 1978). Obviously, if such indices are to be used reliably they must be supported by a diverse data base drawn from both natural and experimental populations.

The major objective of this study was to obtain an integrated view of protein and nonprotein carbon utilization in

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the catabolic and anabolic metabolism of *Leptoxis carinata*. It will examine the effects of season, age, sexuality and trophic input on bioenergetic partitioning in three natural populations. Such data will also provide relevant information regarding the current debate as to which physiological variables are most appropriate for intraspecific comparisons (Russell-Hunter, 1970; 1978; Bayne and Widdows, 1978).

MATERIALS AND METHODS

Leptoxis (= *Spirodon*) *carinata* (Bruguière) is a freshwater snail of the family Pleuroceridae (Order Mesogastropoda: Superfamily Cerithiacea). In New York state, it appears to be restricted to riffle areas in the larger rivers of the Susquehanna drainage (Harman and Berg, 1971). Like all pleurocerids, *Leptoxis* is dioecious and uses a pectinibranch ctenidium for respiration. Like most freshwater snail genera, *Leptoxis* is a grazer of the *Aufwuchs*, the scum flora which covers submerged surfaces in most freshwater habitats. Three populations of *L. carinata* were studied (sample site, abbreviation, altitude in meters, latitude and longitude, county, and U.S.G.S. quadrangle):

Tioughnioga River (TIO), 341 m, 42° 38.34′ N., 76° 11.25′ W., Cortland Co., Homer Quad.—7.5 series.

Susquehanna River (SUS), 341 m, 42° 28.79′ N., 74° 58.75′ W., Otsego Co., West Davenport Quad.—7.5 series.

Unadilla River (UNA), 335 m, 42° 37.59′ N., 75° 19.60′ W. Chenango-Otsego Co. line, New Berlin North Quad.—7.5 series.

The sites are essentially similar, with snails occurring on rocks in areas of continuously flowing water.

Respiration rates were monitored with Clark-type polarographic oxygen electrodes (Clark, 1956). Respiration chamber tubes were modified for small aquatic molluscs by securing a glass ring in the bottom of a tube (Burky, 1977). The ring supports a magnetic stirrer which revolves above the snails for maximum water circulation in the chamber with minimal disturbance to the snails.

Specimens of *Leptoxis carinata* were collected monthly (bimonthly November through April) for 1.5 years at the three sites and returned to the laboratory in insulated containers. In the laboratory, snails were sexed, shell lengths (SL) obtained for separation of generations, and their shells cleaned of epifaunal and algal organisms. They were then held with aeration at field temperatures in an incubator, all respiration experiments being done within four days. For adults (SL>8 mm) rates were determined individually on eight or nine members of each sex selected to span the range of adult shell lengths in the population at that season. Juvenile (SL<8 mm) rates were determined for single individuals or batched groups of measured snails (± 0.5 mm) depending on the magnitude of the rates.

The water used in the experiments was brought from each site at the time of the appropriate collection, held at field temperature, and filtered before being used. The snails were given sufficient time to attach to the chamber walls before placing the magnetic stirrer over them. The start of stirring did not usually disturb attached snails. All respiration rates were done at field temperatures on attached snails. With this apparatus, continuous measurements are made of decreasing values from 100% oxygen saturation. Snails were run for ten to fifteen minutes which normally amounted to about a 15% and never more than a 35% change in percent oxygen saturation.

The same animals which had been used in all respiration experiments were, within 24 hours, used in determination of ammonia excretion rates. These snails were set up individually in 10 ml of filtered river water at field temperatures for three to ten hours, depending on temperature (longer at lower temperatures). After removal of the snails, the ammonia concentration of the water was determined using an Orion Model 95-10 gas sensing ammonia probe coupled to a Corning Model 7 pH/mV meter. Two blanks were measured at the end of each set of experimental tubes. Readings were taken (in mV) one minute after immersion of the probe and addition of 10 M NaOH to bring the sample to pH 11 (Gilbert and Clay, 1973). Samples were constantly stirred and calibration curves were plotted using ammonium chloride standards. A complete set of three standards was done at the beginning of every run and at every twelfth unknown thereafter. In addition, one appropriate standard was run after every third measurement. These standards enabled accurate compensation (± 6%) for any shifts in probe response during a run.

After ammonia determination, experimental snails were relaxed, fixed, and decalcified. Periostracum was removed, gonad condition checked, and tissue dry weight (TDW) obtained.

The contribution of urea to nitrogenous excretion in *Leptoxis* was evaluated once—on UNA snails in September 1979. Ten batches of adult snails were placed in tubes with 50 ml of filtered river water for two hours. The water in each tube was then divided into two fractions. To one fraction was added 0.5 ml of urease solution (five Dunning urease tablets—Sigma Chemical—in 45 ml of distilled water and 5 ml of pH 6.5 phosphate buffer). These urease treated fractions were allowed to react for 15 minutes. Both sets of fractions were then assayed for ammonia using the same procedure described above. Standards included the usual ammonium chloride standards, along with both urea standards with urease, and ammonium chloride standards with urease. Further blanks with and without urease were also measured.

RESULTS

At all three sites, *Leptoxis* is a semelparous biennial with growth largely restricted to two periods: the first three months of life (July through October) and May through August of the second summer (Aldridge, 1982). The latter growth period ends at about the time gametogenesis begins.

Because the size range (tissue mass) within a generation at any one time was less than $10^{0.7}$, weight specific rates of oxygen uptake [μl O_2/ (mg TDW • hr)] and ammonia excretion [ng NH_3/ (mg TDW • hr)] were averaged within generations and used in assessing the effects of season and sex on metabolic rates during a snail's lifespan. Differences between males and females in weight specific rates were evaluated using two tailed t-tests. Figure 1 shows mean weight specific oxygen uptake rates during a modal lifespan at each site. Similarly, Figure 2 shows mean weight specific ammonia excretion rates over a modal lifespan. The rates shown on these figures are derived from the 1977 generation except for the earliest juvenile values (1978 generation). Separate means are shown for males and females where distinct ($P<0.05$).

The patterns of oxygen uptake over each modal lifespan (Fig. 1) are similar for the three populations. Weight specific oxygen uptake rates are highest early in life and lowest during the winter months. Differences between males and females occur during the second fall of life when gametogenesis is taking place and also just prior to reproduction the following spring. Where such sexual differences exist, males always have higher oxygen uptake rates.

The patterns of weight specific ammonia excretion through a modal lifespan (Fig. 2) are again similar for the three populations. The highest ammonia excretion rates occur during the rapid growth phase of the second summer. The sexes are separable in the second fall of life during gametogenesis, again with higher male rates. No significant amounts of urea were excreted.

To better assess shifts in metabolism, oxygen uptake and ammonia excretion were measured nearly concurrently. This allows the computation of the ratio of moles atomic oxygen taken up per hour to moles of N execreted per hour (O:N) for each pair of experiments. This O:N ratio should reflect shifts in catabolic activity with regard to the ratio of protein to carbohydrate and fat being utilized. Low O:N ratio values (<30) suggest the heavy use of protein in catabolism whereas values >50 indicate that carbohydrates and lipids are the primary substrates used in catabolism (Bayne and Widdows, 1978). Figure 3 shows the mean values (normally distributed) of this ratio over a modal lifespan. The pattern of changes in this ratio, though not their magnitude, during a snail's lifespan is similar in the Unadilla and Tioughnioga populations where the ratio becomes depressed during the rapid growth period of the second summer. In contrast, the ratio for the Susquehanna snails is generally higher and varies very little during a snail's lifespan. As already noted, sexually dimorphic shifts in oxygen consumption were paralleled by those for nitrogen excretion during gametogenesis (except for SUS snails). Thus sexual variation in the O:N ratio shows no consistent pattern. However, SUS and UNA prebreeding females have lower O:N ratios than males, which should reflect the utilization of protein stores to meet energy needs when nonprotein resources are needed to provide yolk for eggs (Aldridge, 1982).

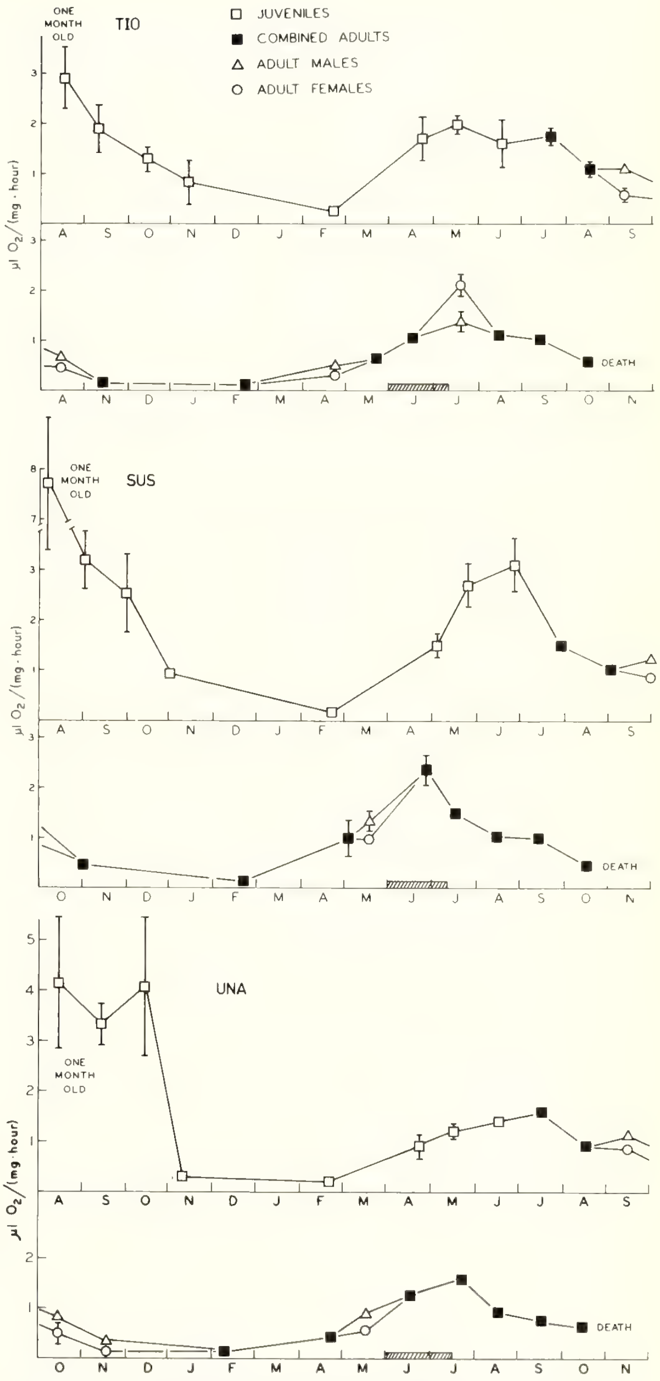

Fig. 1. Mean weight specific respiration rates {μl O_2/ (mg tissue dry weight • hr)} during the lifespan of an average 1977 generation *Leptoxis* individual in the Tioughnioga (TIO), Susquehanna (SUS), and Unadilla (UNA) populations. Juvenile rates are represented by open squares. Where mature males and females have different means ($P<0.05$) males are represented by open triangles and females by open circles. Where the sexes are indistinguishable a combined adult mean is plotted (closed squares). Bars about the means delineate two standard errors and where absent indicate the symbol encloses two standards errors. Egg laying is delineated by the hatched band on the lower abscissa.

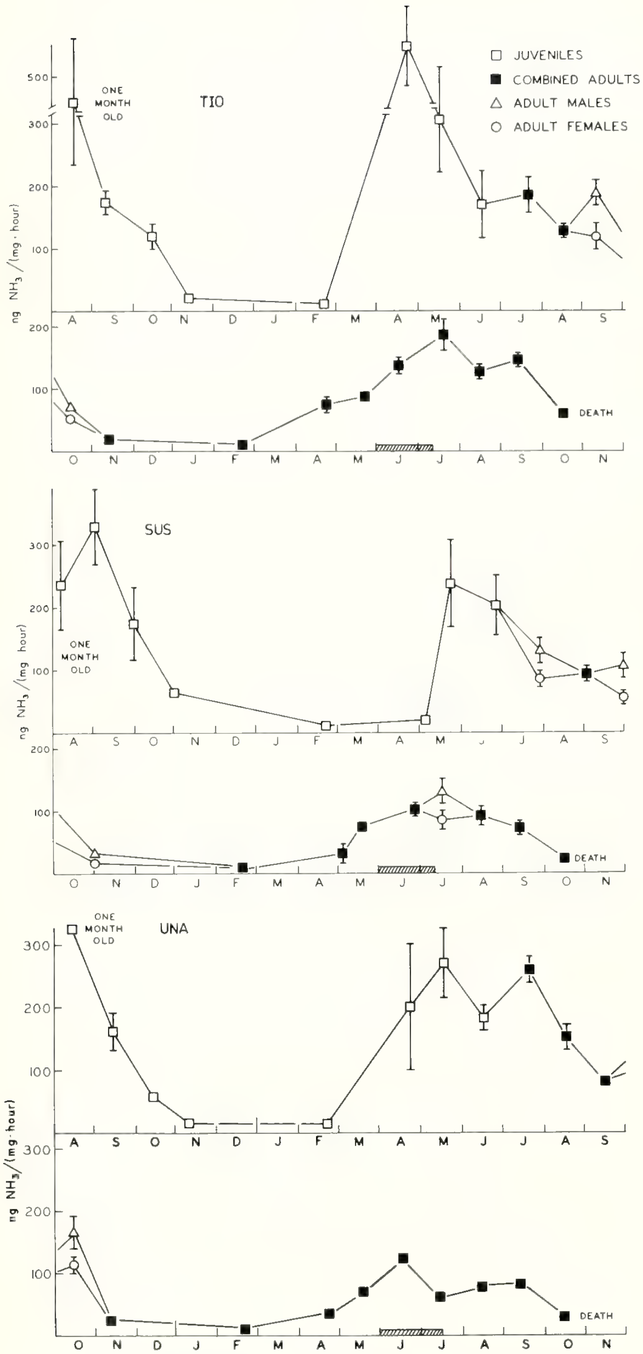

Fig. 2. Mean weight specific ammonia excretion rates {ng NH_3/ (mg tissue dry weight • hr)} during the lifespan of an average 1977 generation *Leptoxis* individual in the Tioughnioga (TIO), Susquehanna (SUS), and Unadilla (UNA) populations. Symbols and conventions as in Figure 1.

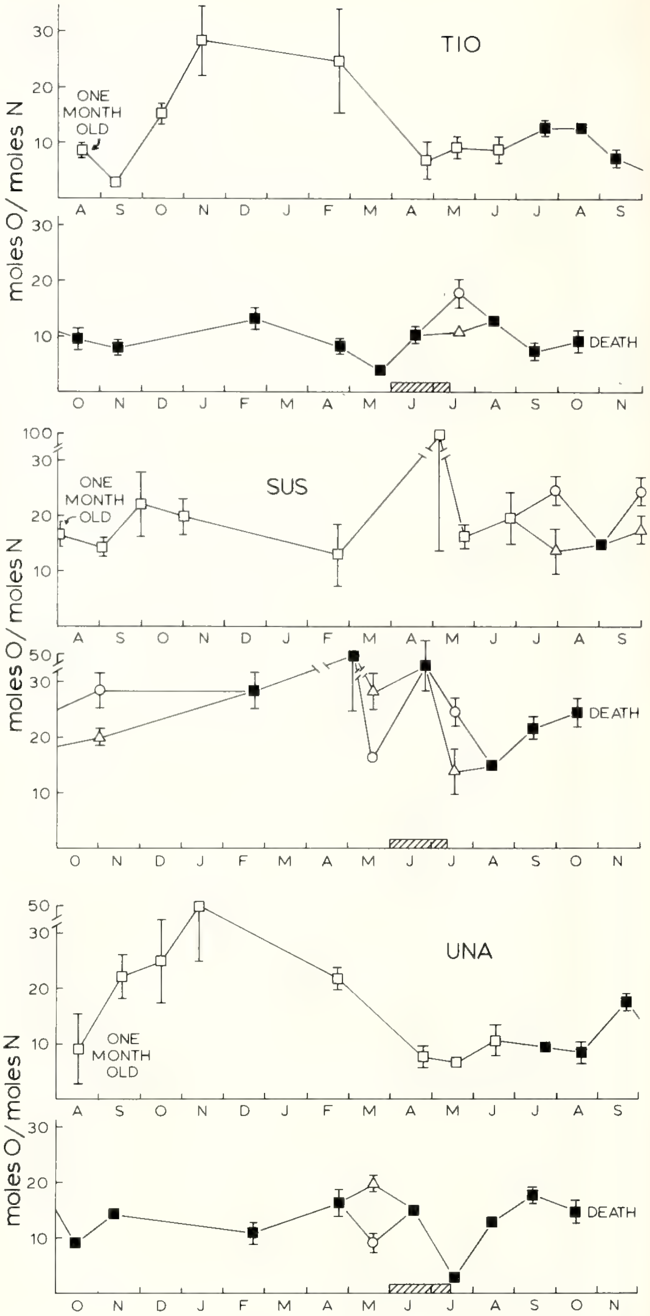

Fig. 3. Mean values for the atomic molar ratios of oxygen consumed to N excreted during the lifespan of an average 1977 generation *Leptoxis* individual in the Tioughnioga (TIO), Susquehanna (SUS), and Unadilla (UNA) populations. Symbols and conventions as in Figure 1.

To provide an integrated picture of a snail's resource partitioning (C & N) during its life cycle, lifespan balance sheets for each population's 1977 generation were calculated. These budgets were computed from the third month of life with males and females treated separately. The terminology and procedures used in this section will follow those set out by Russell-Hunter (1970) and can be summarized by the following equations.

Total Assimilation (TA) = Non-respired Assimilation (N-RA) + Respired Assimilation (RA)

Non-respired Assimilation (N-RA) = Somatic Growth (G) + Gametes (R).

It should be emphasized that estimates of variance for certain values on the budget sheets are not available due to the derived nature of such values.

In all cases the growth component of N-RA (G) will be computed as the difference between the appropriate mean carbon or nitrogen content of a 1977 generation snail during July 1979 and the corresponding spat value in August 1977 (Aldridge, 1982). The reproductive component of N-RA (R) for females was estimated using regressions of lifespan reproductive output versus shell length in conjunction with female shell length distributions during the breeding (Aldridge, 1982).

To estimate respired assimilation (RA) during a mean snail's lifespan, the seasonal regressions of oxygen uptake and ammonia nitrogen excretion rates versus shell length were used in conjunction with the shell length distributions of the 1977 generation in the appropriate collection (Aldridge, 1980). In each case, daily rates of oxygen consumption and ammonia nitrogen excretion were computed for each member of the 1977 generation present in a collection at 2 to 3 month intervals. Within a collection (and for each sex, if mature), the appropriate values were summed and mean daily rates of oxygen uptake and ammonia excretion obtained. To estimate interval rates, the appropriate mean daily rate was multiplied by the number of days in the interval which had been computed for a given collection date (Aldridge, 1980). This was done by halving the sum of the days either side of the data under consideration to the next adjacent collection dates and adding one day. Total values for RA (O_2 or N) during any period of the snail's life cycle can be computed by summing the appropriate interval rates during the time interval under consideration.

To integrate O_2 estimates of RA with the rest of the partitioning measurements requires that they be converted to carbon equivalents. Unfortunately this is not a straightforward matter as different foods can have different respiratory quotients (see, for example, Brody, 1945). However, satisfactory respiratory quotient values can be computed for each seasonal interval by the following equation (Harper et al., 1977):

$$\mathrm{RQ} = \frac{0.95\left[\text{total } \mu\text{l } O_2 \text{ uptake} - (5.92 \bullet \mu\text{gN excreted})\right] + (4.75 \bullet \mu\text{gN excreted})}{\text{total } \mu\text{l } O_2}$$

where 5.92 μl is the amount of O_2 necessary to oxidize the protein containing 1 μg of N which, in turn, will eliminate 4.75 μl of CO_2 per μg N. The assumed nonprotein respiratory quotient of 0.95 is based upon 10% fat and 90% carbohydrate in the nonprotein component of snail respiratory metabolism.

Table 1. Summary of carbon partitioning in *Leptoxis carinata* for an average 1977 generation snail during its lifespan.

	protein C mg		nonprotein C mg	
	TIO			
	female	male	female	male
total assimilation	35.0	35.5	24.3	23.5
respired assimilation	28.0	28.3	23.8	23.5
nonrespired assimilation:	7.0	7.2	0.5	0
growth	6.6	7.2	0	0
reproduction	0.4	—	0.05	—
	SUS			
total assimilation	35.3	37.0	55.1	47.3
respired assimilation	25.7	28.1	52.4	45.8
nonrespired assimilation:	9.6	8.9	2.7	1.5
growth	8.5	8.9	1.7	1.5
reproduction	1.1	—	1.0	—
	UNA			
total assimilation	48.2	49.5	41.4	41.2
respired assimilation	38.0	38.7	40.3	41.1
nonrespired assimilation:	10.2	10.8	1.1	0
growth	9.2	10.8	0	0
reproduction	1.0	—	1.1	—

To obtain the life-time values for protein and nonprotein carbon partitioning set out in Table 1, the lifespan nitrogen budget values produced by the above procedures were multiplied by 3.25, the average C:N ratio of protein (Brody, 1945), to yield TA, RA, and N-RA (G and R) in terms of protein. These values can then be substracted from the appropriate total carbon values of TA, RA, and N-RA to obtain the value for nonprotein carbon. Similar manipulations can be used to convert the productivity and food quality indices of *Aufwuchs* (the snail's food source) presented by Aldridge (1982) to protein and nonprotein carbon equivalents (Table 2).

Protein accounts for 80–95% of the carbon in a snail, depending upon the site and time of year. As a percentage of total assimilated carbon, protein accounts for 60%, 41% and 55% for TIO, SUS, and UNA snails, respectively. The percentages of total assimilated protein used in N-RA were 20.0%, 25.5% and 21.5% for TIO, SUS, and UNA snails, respectively. In females, reproduction accounts for 6–11% of the N-RA protein carbon or 13–19% of the total carbon in N-RA. Protein accounts for 49%, 36% and 51% of the carbon used in RA for TIO, SUS, and UNA animals, respectively. In females, protein accounts for 44% to 52% of the carbon used in reproduction. Regarding the partitioning of nonprotein carbon sources, nearly all the assimilated nonprotein carbon is used in respiration (95–99%). Females use about 2% of their assimilated nonprotein carbon in reproduction.

To obtain the seasonal patterns of carbon partitioning during a snail's lifespan (1977 generation), daily rate estimates for selected periods during the snail's life cycle (Aldridge, 1980) were computed (males and females combined) for protein and nonprotein carbon allocated to RA and N-RA in a fashion analogous to the calculation of the lifespan budget sheets. For RA, this was done by multiplying the

Table 2. Productivity and food quality indices for the three sites ($\bar{x} \pm$ sd).

Aufwuchs Food Quality	TIO	SUS	UNA
C:N	7.3 ± 0.2	5.0 ± 0.2	5.8 ± .01
μg protein C/mg	38.2 ± 8.2	26.7 ± 6.1	28.4 ± 3.9
μg nonprotein C/mg	47.5 ± 4.7	14.7 ± 2.9	22.4 ± 5.0
Aufwuchs Productivity			
mg protein C • m^{-2} • day^{-1}	1.46 ± 0.40	1.66 ± 0.47	3.67 ± 0.87
mg nonprotein C • m^{-2} • day^{-1}	1.74 ± 0.68	0.94 ± 0.52	2.93 ± 0.96

mean interval rates of nitrogen excreted by 3.25 to obtain protein carbon's contribution to RA which is substracted from the total RA carbon to yield the contribution of nonprotein material to RA. Dividing these interval rates by the number of days in the interval converts them to daily rates. Daily rates of protein allocation to N-RA are computed by first taking the mean nitrogen value for a snail at the end of the time interval and subtracting the immediately preceding mean nitrogen value of a snail at the beginning of the interval. This value is then multiplied by 3.25 to give an interval estimate of protein carbon acquisition. An interval estimate of carbon N-RA acquisition is computed in the same fashion. Subtracting the interval rate of protein carbon to N-RA from the interval rate for total carbon yields the interval rate for nonprotein carbon to N-RA. Again, dividing these interval rates by the number of days in the interval yields daily rates for N-RA in protein C and nonprotein C terms.

These lifespan patterns for the relative contribution of protein carbon and nonprotein carbon to RA and N-RA are shown in Figure 4 for UNA, TIO, and SUS. Snails at the three sites have similar patterns with most of the net acquisition of protein carbon by N-RA occurring in the second summer of life, with degrowth in the Susquehanna population (use of structural protein to meet respiratory demands) occurring at times during the winter and early spring. Peak respiratory expenditures occur during the second summer and during breeding. In UNA and TIO snails, protein provides the larger source of carbon used in RA while SUS snails rely more on nonprotein sources.

DISCUSSION

Life-cycle patterns and rates of weight specific oxygen uptake were basically similar in the three populations. Peak weight specific rates declined as the animals age and grow as expected (McMahon, 1983). Seasonally, changes in oxygen uptake were correlated with changes in temperature and reproductive activity as has been shown to be the case in other aquatic herbivores (Bayne and Widdows, 1978; Aldridge, 1983).

The life-cycle patterns of weight specific ammonia excretion are also similar for the three populations. The weight specific rates of ammonia excretion, however, show more interpopulational variation than the oxygen uptake rates. This variability in rates is positively correlated with the availability of protein carbon per mg *Aufwuchs*.

The patterns of the relative use of protein and nonprotein carbon in respired assimilation expressed as such or O:N ratios are broadly similar in the three populations and reflect similar life-cycle patterns and seasonal variation. Earlier work, without data on nitrogen excretion rates, attempted to evaluate shifts in protein and nonprotein catabolism by changes in the C:N ratios of the snail's standing corp biomass (Apley et al., 1967; Apley, 1970; Russell-Hunter, 1970; Burky, 1971; Mattice, 1972; Russell-Hunter et al, 1972; Eversole, 1974; McMahon, 1975; Hunter, 1975; Russell-Hunter and Eversole, 1976; Browne, 1978). The evaluation of the dynamic patterns of protein and nonprotein catabolism from static indices of biomass composition is useful but admittedly simplistic (Russell-Hunter, 1970; 1978). By any criterion, actual rates of oxygen uptake and nitrogen excretion allow the computation of better rate values for protein and nonprotein carbon partitioning. Sex and food quality affect both the relative use of protein versus nonprotein in respired assimilation (RA) and to a lesser extent overall rates of RA. In all populations, the second summer of life (the major growth period) is distinguished by the highest rates of RA expenditures and growth. This period involves a relatively large fraction of RA being derived from protein (reflected by O:N ratios <20). The pattern of O:N ratios in the fall indicates a decrease in the relative amount of protein being used in RA. Nonprotein stores used at this time are subsequently augmented by a modest degree of degrowth later in the overwintering, paralleling similar degrowth in other molluscs (Russell-Hunter and Eversole, 1976; Russell-Hunter et al., 1984). Hence, the relative use of protein versus nonprotein sources in respiration is dependent both on their absolute and relative availability and on the changing energetic demands of the organism. Hence, low O:N ratios in the second summer probably reflect the availability of assimilated protein in excess of anabolic demand whereas low O:N ratios in the fall and winter reflect the use of tissue protein to meet energetic demands which exceed contemporaneous inputs. Some workers have suggested that low O:N ratios are indicative of metabolic "stress" (Bayne, 1973b; Widdows,

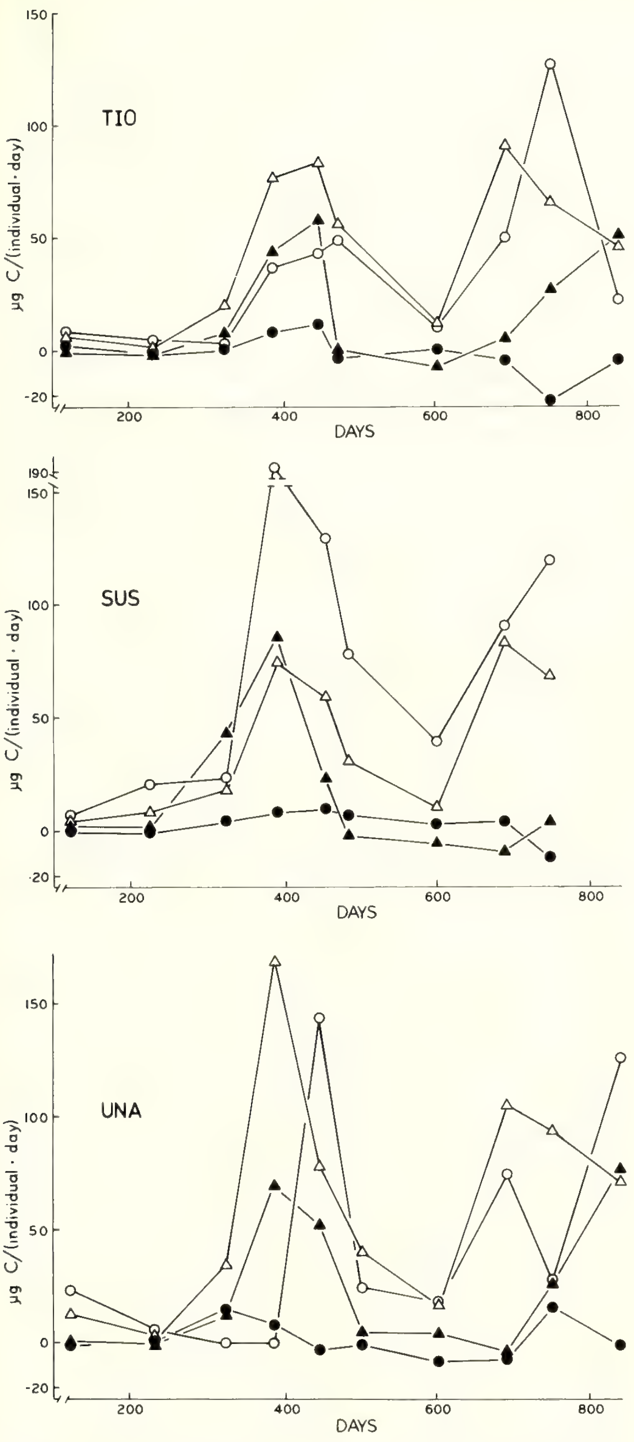

Fig. 4. Daily partitioning rates of protein (triangles) and nonprotein (circles) carbon into respired (open symbols) and nonrespired (closed symbols) assimilation during the lifespan of an average *Leptoxis* individual in the Tioughnioga (TIO), Susquehanna (SUS), and Unadilla (UNA) populations from the fourth month after hatching (day 121) until death.

1978), a conclusion possibly true for *Leptoxis* in later winter, though clearly unlikely during the second summer. These data suggest that the O:N ratio is affected by a great variety of factors such as age, sex, season and is also subject to considerable interpopulational variation in the absence of any obvious environmental "stress."

Regarding nonrespired assimilation (N-RA), the bulk of protein acquisition occurs in the second summer of life. Nonprotein carbon additions to N-RA are maintained at modest but fairly constant levels throughout life.

A major extrinsic source of variation in the bioenergetic partitioning of protein and nonprotein resources appears to be the quality of the *Aufwuchs* (McMahon et al., 1974). The percentage of the total assimilated carbon as protein carbon is inversely correlated to the percent protein composition of the carbon biomass of the *Aufwuchs* while being positively correlated to the *Aufwuchs* protein content per mg. These observations suggest that for this herbivore not only is the ratio of protein carbon to nonprotein carbon of the food important to bioenergetic partitioning (Russell-Hunter, 1970) but that the inorganic component of the food may also be an important determinant of food quality for *Aufwuchs* grazers. It is worth noting that the net growth efficiency of protein carbon (as protein to N-RA/protein to TA) is inversely related to the percentage of the assimilated carbon which is proteinaceous. This probably reflects parsimony with respect to protein which favors the preferential use of nonprotein carbon in RA, thus sparing assimilated protein for anabolic purposes. There are obvious parallels in vertebrate nutritional stress (Brody, 1945; Harper et al., 1977).

Less obvious than the effects of food quality on biomass partitioning, but perhaps more significant, are sexual differences in the allocation of biomass. These patterns reflect different male-female strategies which probably derive from the earlier adaptive divergence of gametes which resulted in more massive and less mobile eggs contrasting with smaller and more mobile sperm (Parker et al., 1972). Russell-Hunter and McMahon (1976) and others (Maynard Smith, 1971; Scudo, 1973; Smith, 1967) have explicitly or implicitly assumed that females increase their fitness (in those species without parental care) by a greater contribution to the next generation in total biomass terms. Strategy of males, on the other hand, involves the reduction of biomass costs while increasing the number of mating encounters with females. Any number of possible tactics for males can be involved, all including either lower energy acquisition rates or higher kinetic expenditures. In *Leptoxis*, the biomass partitioning patterns reflect these divergent male-female strategies to some extent. In all three populations, males show higher weight specific rates of O_2 consumption than females during the mating period, and similarly during the preceding fall while females are in gametogenesis. Also for all three populations, males show generally lower growth efficiencies and less growth than corresponding females. Circumstantial evidence supporting the assumption that males contribute less material resources to the next generation is the observation that postbreeding males are in better condition (carbon content) relative to their prebreeding state than postbreeding females are relative to their prebreeding condition. If females partitioned carbon the way males do during breeding, their postbreeding carbon content values would be, on average, 30% higher than the observed values (Aldridge, 1982).

In conclusion, both quantitative and qualitative variation in partitioning patterns for an individual snail can be attributed to the effects of season, temperature, age, and sex. Sources of interpopulational variation in partitioning patterns are more difficult to analyze. However, data presented here and elsewhere suggest that diet quality is a major source of interpopulational variation.

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PRELIMINARY STUDIES OF PARTICLE SIZE SELECTION BY FILTER-FEEDING SPECIMENS OF THE PROSOBRANCH *BITHYNIA TENTACULATA*

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ABSTRACT

Members of the freshwater prosobranch species *Bithynia tentaculata* have two feeding modes, grazing and filter-feeding. While previous studies have demonstrated the viability of filter-feeding, little work has been completed on the particle size selection by filter-feeding specimens of this species. The present work has two purposes. Firstly, we examine some new methods for measuring clearance rates. Secondly, we provide a preliminary study of particle size retention by the ctenidial filter of *B. tentaculata*. The filterable material employed included naturally occurring suspensions (*Chlorella vulgaris* and *Escherichia coli*) as well as suspensions of uniformly-sized latex beads (polystyrene: 0.497 μ and 1.091 μ; styrene divinylbenzene: 7.6 μ). Clearance rates in suspensions of *Chlorella vulgaris* were comparable to those reported in previous studies which employed the same methodology. In suspensions of styrene divinylbenzene beads, snails had clearance rates which were four to five times higher than those observed in suspensions of *Chlorella*. The styrene divinylbenzene beads are much more uniform in size than the cells from laboratory cultured *Chlorella vulgaris* (2–12 μ). The methods used for estimating clearance rates in *Chlorella* suspensions may provide conservative values for clearance by individual snails. The latex bead methodology should prove useful in future studies of filter-feeding in gastropods, especially since specimens of *Bithynia* did not appear averse to filtering latex particles. We test the hypothesis that filter-feeding individuals of *B. tentaculata* can exploit suspensions of ultraplankton (< 5 μ) and the smaller sized members of the nanoplankton (5–50 μ). Snails had insignificant clearance rates in suspensions of *E. coli* (0.4-1.0 μ) or the two sizes of polystyrene beads. Our results suggest that specimens of *Bithynia tentaculata* can not exploit the ultraplankton or the smaller sized members of the nanoplankton.

A fundamental principle in biology is that all organisms require a constant or intermittent supply of nutrients to maintain physiological integrity. In the phylum Mollusca, the Gastropoda is by far the largest and most diverse class. The success of this class has been attributed in large measure to the "structural and functional plasticity" of the feeding apparatus (Kohn, 1983). One viable avenue of future research will be to increase our knowledge of the links between gastropod feeding and physiological ecology. In particular, an important area of research is the assessment of the relationship of behavioral plasticity in the decision making process to the physiological and morphological constraints on the feeding mode.

The majority of freshwater prosobranchs are herbivores feeding on bacteria, protists, and both macroscopic and microscopic algae. Aldridge (1983) suggests that all prosobranch gastropods are to a greater or lesser extent radular grazers on *Aufwuchs.* The greatest majority of filter-feeding mollusks are lamellibranch bivalves. Very few gastropods are obligate filter-feeders, and there is not a substantial literature base describing the filter-feeders like *Crepidula fornicata* (Orton, 1912a, b; Werner, 1953), *Vivaparous viviparous* (Cook, 1949), *Turritella communis* (Graham, 1938), *Capulis ungaricus* (Yonge, 1938), *Calyptraea chinensis* (Orton, 1912b; Werner, 1953), and *Bithynia tentaculata* (Schafer, 1953; Lilly, 1953; Tashiro and Colman, 1982).

The feeding modes of the prosobranch species, *Bithynia tentaculata*, have been studied by several investigators (Tashiro, 1980, 1982; Tashiro and Colman, 1982; Mattice, 1970; Starmuhlner, 1952; Lilly, 1953; Russell-Hunter, 1957). Specimens of *Bithynia tentaculata* procure organic substrate through two feeding strategies, grazing on *Aufwuchs* and

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filtering of suspended materials (Tashiro and Colman, 1982). The preliminary studies reported in this paper were designed to assess particle size selection by individuals of *Bithynia* while they were filter-feeding. These studies complement analyses of feeding and bioenergetic partitioning of ingested materials by members of a *Bithynia* population from Oneida Lake (New York, USA).

Some workers have debated the proportionate role of filter-feeding in nutrient acquisitioning by individuals of *Bithynia tentaculata*. Tashiro and Colman (1982; but also see Mattice, 1970, and Fretter and Graham, 1962) discussed the early literature which describes filter-feeding in *B. tentaculata*. Early studies demonstrated that filtering of material from the pallial water currents occurred and that this filtered material was concentrated in a ciliated groove which traverses the floor of the mantle cavity. Concentrations of particles were observed at the exhalent end of the ciliated groove and Schafer (1952) was the first to report observations of *Bithynia* eating these particles. Various viewpoints have been expressed about the importance of filter-feeding in individuals of *B. tentaculata*. These range from the contention that filter-feeding provides only a supplement to grazing (Werner, 1953; Fromming, 1956; Harman, 1968a, b) to the idea that in some populations all or most food is obtained by the filtering mode (Russell-Hunter 1957; Mattice, 1970; Tashiro and Colman, 1982). Recently, Tashiro and Colman (1982) provided evidence which suggests that individuals of *B. tentaculata* do filter-feed and that relative to grazing, filter-feeding allows members of this species to accrue a higher net gain of nitrogen (= protein) and carbon per respired cost. Such evidence comes from a comparative partitioning approach which assessed net nutrient gains obtainable by filter-feeding and grazing.

The primary focus of this work was to assess clearance rates for two organic substrates (*Chlorella vulgaris*, 2–12 μ, and *Escherichia coli*, 0.4–1.0 μ diameter) and also for three sizes of uniform latex particles (0.497 μ, 1.091 μ, and 7.6 μ). We were interested in both age- and sex-specific patterns of particle retention, but we also wanted to compare the potential for filtering materials available in natural freshwater habitats (phytoplankton and bacteria) with the potential for filtering nonbiogenic materials in the same size range (latex beads).

Very little work has been done on the particle size selection of filter-feeding gastropods. Tashiro and Colman (1982) showed that specimens of *Bithynia tentaculata* can filter *Chlorella vulgaris*. Other workers have suggested that individuals of *B. tentaculata* can filter particles the size of bacteria (see Mattice, 1970, and references within). The ctenidium of *Bithynia* is large and the lamellae are triangular. Each lamella has a broad base and the tip overhangs a ciliated groove traversing the floor of the mantle cavity (Fretter and Graham, 1962). While members of this species undoubtedly graze, the frequency of filter-feeding seems to depend on the abundance of grazeable substrates, but also on the nature of materials suspended in the water (Tashiro and Colman, 1982). Hypotheses derived from foraging theory generally assume that animals are "efficient" in their foraging activities. It is intuitively reasonable that natural selection favors the most economic of alternate foraging patterns and that such selection has played a major role in the evolution of predator foraging behavior. Filter-feeding may be more efficient in terms of net yield of nutrients per unit time feeding, but this contention is based only on the results of studies which utilized *Chlorella vulgaris* as filterable material. Temperate lentic habitats typically have seasonal fluctuations in phytoplankton populations. The qualitative and quantitative facets of planktonic assemblages are idiosyncratic to a particular aquatic system, but in any case, the planktonic interactions are complex and dynamic. By delimiting the particle sizes which specimens of *Bithynia tentaculata* can filter, the relative importance of filter-feeding in this species can be contextualized in the framework of the most probable availability of filterable materials. We present data which suggest that specimens of *Bithynia tentaculata* may not be able to exploit the smaller nanoplankton and bacteria of fresh waters.

MATERIALS AND METHODS

Specimens of *Bithynia tentaculata* were obtained from their natural habitat in Oneida Lake. Individuals were chosen from a population site which previously had been studied by Mattice (1970), Tashiro (1980), and Tashiro and Colman (1982). The habitat description can be found in a number of sources, notably the review by Mills et al. (1978; but also see Mozely, 1954; Harman and Forney, 1970; Russell-Hunter, 1970).

Snails were obtained from an area close to Shackleton's Point, Oneida Lake (New York, USA: N 43° 10.42′, W 75° 55.49′). Specimens were shipped to Gambier, Ohio, via air freight and arrived in excellent condition (greater than ninety percent survivorship). Animals were placed in the experimental environment one day after arrival.

Individuals were separated by sex and age, and were placed into an environmental chamber. Males were distinguished by an obvious penis and flagellum which emerge into the mantle cavity, just posterior and right dorsolaterally to the head (Tashiro, 1980). Growth lines, which appear to result from weathering of the shell aperature lip during the winter (Tashiro, 1980) were used to separate age classes. Aquariums contained fresh pond water (changed every third day) and were supplied with air. A twelve hour light/dark cycle was maintained. Fresh pond water was obtained from a spring fed pond near Gambier, Ohio. This pond supports large populations of mollusks. Artificial food discs, providing a high protein/low ash diet, were prepared according to the recipe described by Tashiro, Aldridge, and Russell-Hunter (1980). This ration contains powered lettuce, Brewers yeast, and casein in an insoluble Calcium-alginate matrix.

Suspensions Used for Clearance Rate Studies

Three types of filterable materials were employed in this study—laboratory cultured *Chlorella vulgaris*, laboratory cultured *Escherichia coli*, and latex beads. Tashiro and Colman (1982) reported that the *Bithynia tentaculata* population in Oneida is exposed to suspended materials (phytoplankton and detritus) at concentrations close to 4.11 mg · l^{-1} (dry weight; SD = 1.56, N = 8). All of the filter-feeding studies reported in the present work use concentrations of filterable material close to the concentrations found in the natural habitat from which the experimental animals were taken. Filtration rates are the volumes of water passing through the gill filaments per unit time, while clearance rates are measures of the water volume depleted of particles per time. If a gill has a retention efficiency of 100 percent, then filtration rates and clearance rates are equal. Our work provides estimates of clearance rates.

Chlorella vulgaris cultures (Strain 398; The University of Texas at Austin Collection, Starr, 1964) were grown in Bristol's Solution and maintained under constant illumination. Aliquots were harvested from cultures in exponential growth to provide algae suspensions for filter-feeding studies. Concentrations of *Chlorella*, at 150,000 cells · ml^{-1}, were used in these studies, providing suspensions similar in dry weight per liter to average phytoplankton and detritus suspensions at the *Bithynia* population site (Tashiro, 1980; Tashiro and Colman, 1982).

Escherichia coli cultures were started from mother cultures and grown in 8 ml of Trypticase Soy Broth for four hours at 37°C. Experimental cultures were begun with transfers into sterile T. S. Broth which were grown for four hours. This procedure provided bacteria in the exponential phase of growth. Bacteria cultures in exponential growth phase predominantly contain living cells. From size estimates of bacteria, we calculated that a concentration of 90×10^4 cells · ml^{-1} would yield suspensions equivalent to our *Chlorella vulgaris* cultures in terms of dry weight per liter.

Three different sizes of uniform latex beads (either Polystyrene or styrene-divinylbenzene) were purchased from Dow Diagnostics (Duke Scientific Corporation. Palo Alto, California 94303). Polystyrene beads of two sizes were used: 1.091 μ (SD = 0.0082 μ) , 0.497 μ (SD = 0.059 μ). The styrene-divinylbenzene particles were larger, 7.6 μ (SD = 2.0 μ). These latexes have been found to have near neutral buoyancy in water with specific gravities of nearly one at 25°C (Bangs and Kenny, 1976; Burky and Benjamin, 1979). Beads were supplied at 10% (w/w) aqueous suspension.

Clearance Rate Experiments

Chlorella and *E. coli* suspensions

A method for the measurement of *Chlorella vulgaris* filtration rates by *Bithynia tentaculata* has been described previously (Tashiro, 1980; Tashrio and Colman, 1982). Freshly obtained pond water was filtered through glass wool, then through two grades of millipore filters (sizes 8.0 μ, 0.45 μ). This filtered water was autoclaved at 130°C (20 lb · in^{-2}) for 40 minutes. Algae cultures grown in Bristol's solution were diluted with filtered pond water to obtain a minimum concentration of 150,000 cells · ml^{-1}. Acid-washed 50 milliliter beakers were used as experimental chambers. Each chamber was partitioned by a perforated plastic disc so that a magnetic stirring bar could be placed in the bottom. The stirring bar kept algal suspensions from settling, without disturbing the animals. Snails were pre-fed. Pre-feeding consisted of allowing individuals to filter undisturbed for thirty minutes. After pre-feeding, the experimental chambers were rinsed several times with the algae suspension and then filled with forty milliliters. An individual animal (female or male, one- or two-year-olds) was introduced into an experimental chamber and clearance rates were measured. Controls consisted of filtered pond water and algae in the feeding chamber. Changes in algae concentrations were assessed by measuring the amount of algae in the feeding chamber at five time intervals: 0, 10, 20, 30, and 40 minutes. Algal concentrations were quantified using a hemocytometer (nine cells of 0.1 mm^3 volume at each time interval).

Clearance rates were determined using a regression technique. Algal concentrations were regressed against time, using a least squares linear regression (See Table 1). The slope of the least squares line yielded a rate of change in algae cell concentrations. This rate was used to calculate a clearance rate (milliliters filtered/milligram tissue dry weight · hour).

Estimates of clearance rates were standardized for weight by using tissue dry weights of individual snails. Animals were fixed with 12% neutral formalin (saturated with

Table 1. Equations used to calculate clearance rates in suspensions of *Chlorella vulgaris*, *E. coli*, and latex beads.

Suspension	Clearance Rate Equations
Chlorella vulgaris	$C = S_r(60 \text{ min} \cdot \text{hr}^{-1})(E_v)/I$
E. coli and Latex Beads	$C = S(60 \text{ min} \cdot \text{hr}^{-1})(E_v)/I$

S_r = slope of least squares line, the rate of change in *Chlorella* cell concentration (cells · ml^{-1} · min^{-1})
S = rate of change in cell or bead concentration; this value was calculated by substracting the post-filtering concentration from the pre-filtering concentration and dividing the result by the time spent filtering
E_v = volume suspension in feeding chamber: 40 ml for *Chlorella* and *E. coli*, 55 ml for latex bead suspensions
I = Prefiltering concentration in experimental chamber (cells · ml^{-1})

$CaCO_3$) after a filtering experiment. Shells were dissolved in 12% (v/v) concentrated nitric acid (8.5% HNO_3) and the periostraca were removed. Tissue was then dried to constant dry weight in an oven (80°C) (Tashiro, 1980; Tashiro and Colman, 1982).

We developed a relatively simple method for assessing clearance rates for bacterial suspensions. Preliminary studies with individual snails showed no decrease in the concentration of bacteria during 30 minute feeding trials. For two reasons, we batched snails of the same age and sex to assess filtering of bacteria. Firstly, although the bacteria were not multiplying significantly during the first 30 minutes, longer experimental runs would involve error from increases in bacteria number while shorter runs would involve too many snails per batch. Secondly, we were concerned about the reintroduction of bacteria from fecal material that has passed through the gut during the period in which we were measuring filtering. We therefore put five snails in each experimental chamber, all from the same age and sex category, running filter-feeding trials for 30 minutes. Snails were initially pre-fed for 30 minutes with a concentration of *Escherichia coli* (90×10^4 cells · ml^{-1}). A second volume of 0.45 μ filtered and twice autoclaved pond water, was prepared with a concentration of *E. coli* identical to that in the pre-feeding chamber. The experimental volume was poured into sterile (autoclaved) feeding chambers several times to preclude loss of bacteria from adhesion of cells to the glass walls. This volume was then agitated for several minutes. Five snails were placed into each experimental feeding chamber. When all snails were extended from their shell, the timer was started and a 0.1 ml aliquot was removed. Aliquots were serially diluted (10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}) in sterile distilled water and 1 ml was plated on Plate Count Agar. Triplicate trials were performed. A second sampling of aliquots was removed after 30 minutes. These aliquots were also plated. The control consisted of pond water with the identical bacteria concentration. No increases or decreases in concentrations of *E. coli* were observed in the control chambers.

Table 1 shows the equation used to calculate clearance rates of snails in bacterial suspensions. The differences between initial and post-filtering concentrations were used to estimate a decrease in numbers of bacteria over the thirty minute feeding period. Clearance rates were made weight specific by quantifying the tissue dry weights of all five snails in each chamber (see *Chlorella* section above).

Latex Bead Suspensions

An accurate microassay for measuring filtration rates using uniform latex beads has been described by Burky and Benjamin (1979). Three sizes of latex particles were used: 7.6 μ, 1.091 μ and 0.497 μ. Prior to the running of experimental trials, the latex material was agitated at 90–100 oscillations per minute (to uniformly disperse beads). All of the glassware was acid washed with diluted hydrochloric acid, and detergent washed with Alconox and rinsed. The glassware was immediately covered with tinfoil to assure no contamination.

Immediately prior to each experiment a one liter suspension of particles was prepared. Latex particles were volume weighed then diluted into one liter of 0.45 μ millipore filtered pond water. Standard curves were established with each run. We used experimental concentrations which yielded suspensions similar in dry weight per liter to average phytoplankton suspensions at the *Bithynia* population site. Fifty-five milliliters of the experimental concentration were poured into the feeding chamber (50ml beakers). There were three regimes: experimental, control, and blank. The experimental setup contained a snail (male or female two-year-old) with pond water and latex particles, the control had no snail, and the blank was pond water without beads. Only two-year-old snails were used in this preliminary study. This age group was chosen so that comparisons could be made to *Chlorella* clearance rate data in this work, but also to the clearance rates of the two-year-old *Bithynia* used by Tashiro and Colman (1982).

Each snail was placed into a pre-feeding regime (50ml beaker) and allowed to acclimate and filter for 30 minutes. After pre-feeding, snails were placed into the experimental chambers for twenty minutes. Fifteen milliliter aliquots were removed from each of the chambers (the experimentals, the control and blank). Aliquots were drawn from the top of the chamber to avoid "pseudofeces" (Burky and Benjamin, 1979). This volume was dried for 12–24 hours in individual 250 milliliter foil covered beakers at 98°C. Each beaker was then extracted with three milliliters of Dioxane. Using a four-milliliter cuvette absorption values were read against pure Dioxane with a Varian Spectrometer at optimal absorption values; 253 nm (0.05 slit) for Polystyrene particles and 248 nm (0.05 slit) for styrene-divinylbenzene particles (determined by scanning UV absorption range with a Varian Spectrometer). All absorption values were corrected for "background" due to residues in pond water.

A standard curve was constructed using three concentrations of beads: 25% (by weight) below the experimental concentration, the experimental concentration, and 25% above the experimental concentration. This curve provided a regression for absorption versus concentration of particles.

Post-filtering concentrations were determined by using the standard curve. The concentration difference between pre-filtering and post-filtering samples was divided by the time of filtering to yield the equivalent of a rate of bead removal. This rate was used to calculate bead clearance rates (see Table 1 for details). All rates were converted to weight-specific values.

RESULTS

Clearance rates for *Chlorella* and *E. Coli* Suspensions

Chlorella vulgaris concentrations in experimental chambers were determined prior to and during filter-feeding by individual snails. Control chambers during this time period were also examined. Means and standard deviations for each of these counts were calculated. A trend of decrease during the first twenty minutes was consistently observed in chambers with snails. No significant decreases of *Chlorella* concentrations were measured in the control chambers.

Age and sex classes were compared by examining mean weight-specific clearance rates. These rates for *Chlorella* suspensions ranged from 4.1 to 8.5 ml · mg^{-1} (see Table 2). A two-way analysis of variance was used to assess the effects of age and sex on clearance rates. There were clearly differences among the four age-sex classes (male and female, one- and two-year-olds), with age effects being significant (P = .005; see Table 3). The effects of sex and the two-way interaction (sex and age) were not significant. Grouping individuals by age, a t-text was used to compare one-year-old animals (combined males and females) with two-year-olds. This age-specific comparison indicated that one-year-old snails have significantly higher clearance rates than two-year-olds (t = 3.32, p = 0.006).

Our data suggest that specimens of *B. tentaculata* are not filtering significant amounts of *E. coli*. For males, there were no significant decreases in bacteria concentration during the feeding trials. The clearance rates for females were about one-third those observed in the respective age groups of the *Chlorella* experiments. Female clearance rates ranged from 1.25 to 2.33 ml^{-1} · hr^{-1}.

Clearance Rates for Latex Bead Suspension

Filter-feeding studies with latex bead suspensions provides results which were consonant with the data obtained from the *Chlorella* and *E. coli* clearance rate experiments. Only two-year-old animals were used in the latex bead experiments. Neither males nor females cleared the smaller latex beads (polystyrene: 0.497 μ and 1.09 μ), but the larger beads (styrene-divinylbenzene: 7.6 μ) were cleared by both sexes.

During 30 minute trials in suspensions of 0.497 and 1.09 μ diameter latex beads, specimens of *Bithynia tentaculata* did not significantly alter the concentration of beads in the experimental chambers. However, in suspensions of the 7.6 μ diameter beads, concentrations decreased during the filter-feeding trials yielding higher clearance rates than those obtained by specimens of *Bithynia* filtering *Chlorella* (see Table 2). The mean clearance rates for males and females were not significantly different (t-test, P = 0.58). Clearance rates for the 7.6 μ beads were about three to four times the clearance rates in suspensions of *Chlorella*. Combining males and females (two-year-olds), the latex experimental animals had a mean clearance rate significantly higher than the mean rate of combined males and females of the respective age group in the *Chlorella* regime (t-test, P < .001).

Table 3. Two-way analysis of variance for data from filter-feeding experiments in *Chlorella* suspensions.

Source of Variation	Sum of Squares	df	Mean Square	P
Main Effects	55.9	2	27.9	.009
Sex	6.6	1	6.6	.231
Age	47.1	1	47.1	.005
Two-way interactions	1.1	1	1.1	.623
Explained	57.0	3	19.0	.020
Residula	64.2	15	4.3	

Our *Chlorella* clearance rate data is similar to the values obtained by Tashiro and Colman (1982). We feel that the three- or four-fold differences between *Chlorella* clearance and latex bead clearance may be explained, at least in part, by the size distributions of the respective particles. *Chlorella vulgaris* cells can range in size from 2–12 μ (Bold and Wynne, 1978). The styrene-divinylbenzene beads are fairly uniform latex particles. The mean diameter is 7.6 μ (SD = 2.0), but the distribution of sizes and the majority of particles probably fall within a narrower range than do the *Chlorella* cells. We could have obtained conservative estimates of clearance rates for *Chlorella* suspensions if the smaller *Chlorella* were not filtered.

DISCUSSION

Bayne and Newell (1983) but also Jorgensen (1966, 1975) and Winter (1978) have summarized much of the literature describing filter-feeding by bivalve species. The rates of water transport and the gill porosity in bivalves have been reviewed by Jorgensen (1975). Probably, gill function is at

Table 2. Clearance rates for snails in suspensions of *Chlorella vulgaris* or styrene-divinylbenzene beads(ml · mg^{-1} · hr^{-1}).

	Female		Male	
	Two year	One year	Two year	One year
Chlorella vulgaris	4.11 ± .77 N = 5	6.75 ± 2.19 N = 4	4.83 ± 1.99 N = 5	8.45 ± 2.51 N = 5
Styrene-divinylbenzene	20.87 ± 5.93 N = 4		18.90 ± 2.37 N = 5	

least partially controlled by neural inputs. Muscular action and blood pressure may also control gill porosity in bivalve gills (Bayne and Newell, 1983). The analogous studies of gastropod gills have not been completed.

Clearance rates are an indirect estimate of filtration rates. The filtration rate can be defined as the volume of water actually passing through the gill filaments per unit time. Clearance rates are measures of the volume of water depleted of particles over time. If all particles are retained by a gill filter, clearance rates will equal filtration rates (see Jorgensen, 1966; Coughlan, 1968; Burky and Benjamin, 1979). In the literature, there are reports of two general rate responses to particle concentrations. One response is that clearance rates vary inversely with the concentration of suspended materials (Monakov, 1972; Jorgensen, 1975; Winter, 1978; for a gastropod case see Tashiro and Colman, 1982). A second response is observed in some bivalves which maintain clearance rates seemingly independent of the suspension concentrations, even when concentrations are varied over a broad range (Ali, 1970; Jorgensen, 1966, 1975). Perhaps there are a number of potential filtering strategies, each with patterns of responses to particle concentrations and water transport rates (Burky, 1983). Specimens of *Bithynia tentaculata* appear to have an inverse relation between concentration of filterable material and clearance rates, as particle concentration decreases there is at least some compensation with higher clearance rates (Tashiro and Colman, 1982). However, the ctenidium of *Bithynia* is probably the major respiratory surface and there are clear shifts in respiration during each year as snails enter diapause, breeding, and pre-winter physiological states (Tashiro, 1982). There is a need for more work on the physiological ecology of filter-feeding gastropods, especially relative to seasonal bioenergetic patterns and the proprotionate role of filter-feeding if the snails are also grazers.

While there is considerable controversy over the efficiency of particle retention by lamellibranch bivalves, Jorgensen (1975) stated that the lamellibranchs show little difference in particle retention capabilities when filterable particles are in the size range of 1-200 μ. Mohlenberg and Riisgard (1978) examined the particle retention efficiencies of 13 suspension feeding marine bivalve species. For 11 of these species, particles larger than 4 μ in diameter were completely retained, and the retention efficiency decreased only slightly for particles in the 2–4 μ range (75% to 90% retention). There was considerable variation among the bivalves for retention of particles smaller than 2 μ, but the most efficient species retained 70% of the 1 μ particles. Moore (1971) and Jorgensen (1975) proposed that cilia structures on the gill filaments of *Mytilus edulis* (Bivalvia) should create a filter with mesh sizes between (0.6×2.7) μ and $(1\text{-}1.5 \times 3)$ μ, implying that the ctenidium of *Mytilus* could conceivably retain particles between 0.6 and 1.5 μ. Significant retention of this size range of particles was not observed by Mohlenberg and Riisgard (1978) in specimens of *M. edulis*. Both Vahl (1973a, b) and Jorgensen (1975) have emphasized that retention efficiency in bivalve gills probably depends on the integrated activity of all cilary systems on the ctendium. In our work on specimens of *Bithynia tentaculata*, we have not found evidence of retention for particles in the size range of 0.4 to 1.0 μ. These results are consonant with the findings of many studies on bivalve suspension feeding.

Fretter and Graham (1962), Mattice (1970), and Tashiro (1980) have discussed various observations of feeding behavior in individuals of *Bithynia tentaculata*. Initial work by Starmuhlner (1952) and Lilly (1953) demonstrated that filtering of material from the pallial water currents occurred and that filtered material was concentrated in the ciliated groove which traverses the floor of the mantle cavity in this species. The importance of filter-feeding relative to grazing has been debated for the species *Bithynia tentaculata*. Fretter and Graham (1962) and Harman (1968a, b) suggested that filter-feeding can be a feeding mode supplemental to grazing (on *Aufwuchs* and macrophytes). An alternative viewpoint has been expressed (Russell-Hunter, 1957; Mattice, 1970; and Tashiro and Colman, 1982). Russell-Hunter (1957) and Mattice (1970) hypothesized that in some populations all or most of the food is obtained by filtering. Both workers had observed individuals of *Bithynia* in sedentary states, existing without any apparent grazing activity. More recently, this notion has been supported by the studies of Tashiro (1980) and Tashiro and Colman (1982). These workers noted that specimens of *Bithynia tentaculata* in Oneida Lake spend the majority of their nondiapause period as sedentary filter-feeders, attached to the undersurfaces of rocks in the interstices of rocky substrates.

Tashiro (1982) and Tashiro and Colman (1982) contend that discrepancies in the literature reflect the differences in suspended materials which can be used for food by populations of *Bithynia tentaculata*. Tashiro (1980, 1982) has demonstrated that specimens of *Bithynia* can live and reproduce solely on grazeable substrates without resorting to filter-feeding (also see Chung, 1984). Importantly, however, the bioenergetics of filter-feeding provides a higher net gain of nutrients that can be gained by grazing.

Assessments of filtering rates show that individuals of *Bithynia tentaculata* may compensate for lower concentrations of suspended material by increasing rates of particle clearance. Within certain limits, specimens of this species can compensate for lower concentrations of suspended material by increasing filtering rates. At a concentration of 25,000 cells $\cdot$ ml^{-1} *(Chlorella vulgaris)*, a two-year-old female will clear 1.6 times the volume cleared at a concentration of 150,000 cells $\cdot$ ml^{-1} (Tashiro and Colman, 1982).

Investigations of nutritional resources and their size ranges were performed using *Chlorella vulgaris* and *Escherichia coli*. Most freshwater systems contain planktonic algae and bacteria and these organisms could serve as food sources with the potential to provide essential nutrients, especially protein (see Tashiro, 1982). The largely algal nanoplankton (5–50 μ) and the primary bacterial ultraplankton (< 5 μ) can constitute a significant resource for freshwater filter-feeding molluscs. The nanoplankton can constitute 50% or more of the photosynthetic capacity of the phytoplankton.

In eutrophic lentic waters, bacteria may be present in high concentrations. For many fresh waters, a significant food resource is available to filter-feeders if they can exploit the smaller species of the nanoplankton and the bacteria of the ultraplankton. While there are dramatic seasonal fluctuations in the phytoplankton crops of most temperate fresh waters, some components of the nanoplankton may be more constant in both biomass and species composition (Fogg, 1975).

This present work has shown that clearance rates of *Chlorella vulgaris* cells were similar to those reported by Tashiro and Colman (1982) in specimens of *Bithynia tentaculata*. No significant differences were observed between clearance rates of males and females in the same age class. Clearance rates of one-year-old snails (males plus females) were significantly different from those of two-year-old snails. Younger snails had higher clearance rates. Clearance rates for the 7.6 μ diameter latex beads (Styrene-divinylbenzene) were several times faster (roughly 4–5 times) than those observed in the *Chlorella* suspensions. However, the clearance rates of 0.497 and 1.091 μ latex beads were negligible. We do not feel that specimens of *Bithynia tentaculata* can exploit bacteria in the size range of *E. coli*. Our data from feeding studies using *E. coli* suspensions support the results of the latex bead experiments.

Particle sizes for *Chlorella vulgaris* range from 2–12 μ (Bold and Wynne, 1978). Styrene-divinylbenzene beads were 7.6 μ (SD = 2) in diameter. Faster clearance rates within the uniform latex particles may be indicative of a size selection for particular sized "cells." The clearance rate estimates for *Chlorella* could be low if smaller sized *Chlorella* cells were not filtered by the ctenidium of *Bithynia*. Quite probably, the size range in *Chlorella* cultures is greater than the size range in the latex beads. Our studies have examined the potential exploitation of small suspended materials in aquatic ecosystems by filter-feeding specimens of *Bithynia tentaculata*. Using *E. coli* as representative of "small" particulate suspensions, our results suggest that specimens of *Bithynia tentaculata* do not have ctendial adaptations to filter substrates in the size range of small nanoplankton and the ultraplankton (< 2 μ).

The use of uniform latex particles seems to provide accurate measures for clearance rate delimitation. The various size ranges will be useful in the further assessment of particle size selection by filter-feeding specimens of *Bithynia tentaculata*. Application of this method should allow us to answer questions regarding changes in feeding strategies during annual and life-span periods. Experiments utilizing latex beads should help bridge the gaps in our understanding of the interrelationships between physiological logistics, ecology, and life history strategies.

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A REVIEW OF METABOLISM IN THE PISIDIIDAE WITH NEW DATA ON ITS RELATIONSHIP WITH LIFE HISTORY TRAITS IN *PISIDIUM CASERTANUM*

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ABSTRACT

The influence of body size, factors such as temperature, season and O_2 availability on the metabolic rates of pisidiid clams is examined. Published data on metabolic rates are available for 34 populations of these clams covering 21 species of the 3 major genera in this family (*Musculium, Pisidium, Sphaerium*). The value of b from the metabolic rate—weight equation, $\mathring{V}_{O_2} = aW^b$ varies from 0 to 1.24 in this group indicating that metabolic rate may be constant regardless of size ($b = 0$) or that metabolic rate increases proportionately with size ($b = 1$). Values of b within the Pisidiidae can vary intraspecifically and even seasonally within a single population. However, intergenerically there are no significant differences in b-values when metabolic rates measured at 20°C are used. A common b-value of 0.90 applies across all genera at 20°C.

Q_{10}-values vary from 0.2–14.8 within the Pisidiidae, with no significant difference exhibited between genera. Q_{10} can vary with size, season and temperature within populations. The most common acclimation patterns exhibited are Precht Type I (over compensation) and Type V (reverse compensation). However no one pattern applies to a specific group and shifts in acclimation patterns allow animals to efficiently exploit prevailing environmental conditions.

O_2 availability has a profound effect on metabolic rate with low O_2 availability depressing O_2 consumption rates. There is some evidence which indicates that pisidiids may utilize a number of anaerobic metabolic pathways to supplement metabolism at low O_2 concentrations.

The production efficiency (production-to-assimilation) ratio ranges from 10 to 79% in the Pisidiidae with no significant intergeneric differences. There are however significant intergeneric differences in weight-specific metabolic rates with members of the genus *Pisidium* having lower rates than either members of *Musculium* or *Sphaerium*. This, coupled with a similar production efficiency, leads to a lowered production-to-biomass (P:B) for *Pisidium* and may have far reaching effects on the reproductive habits of this genus.

New data on intraspecific variation in metabolism for *Pisidium casertanum* is given. *P. casertanum* from soft water habitats have greatly reduced metabolic rates, possibly in response to lowered ion availability. This lowered metabolic capacity is accompanied by smaller sized individuals and reduced reproduction in the population from soft water habitats.

It appears then, that there is a strong correlation between levels of metabolism and life history traits both intergenerically (*Pisidium* vs. *Musculium* and *Sphaerium*) and intraspecifically (low ion availability vs. high ion availability environments).

Physiologically, organisms can be viewed as energy transformers, they take in energy and apportion it to such processes as metabolism, growth or reproduction. Natural selection acts to optimize the partitioning of energy in order to maximize the fitness of the organism (assuming that there is heritable variability in energy partitioning). It is well known that of the energy assimilated by organisms, the majority is lost as heat through metabolic processes. This does not mean that this energy is wasted, for metabolism encompasses all life sustaining processes including the cost of energy acquisition, defence, locomotion, maintaining cellular homeostasis, etc. Despite the importance of these life sustaining processes, the energy utilized in metabolism is not available to the organism for growth and reproduction. Consequently this energy is not available for the production of young, and thus there must be a balance between the demands placed on assimilated energy in order to optimize fitness (see Russell-Hunter, 1978; Townsend and Calow,

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1981, and Russell-Hunter and Buckley, 1983 for further discussion of bioenergetic theory).

Humphreys (1979) has indicated that the multicellular ectotherms display a great deal of variation in the percentage of assimilated energy that they partition to respiration (58–93%). This indicates, then that the energy available for growth and reproduction varies considerably in the ectotherms. A number of factors can influence the rate of metabolism in ectothermic animals. These include body size, temperature, season, reproductive status and oxygen availability among others.

In this paper I will consider the influence of a number of factors on the metabolic rates of pisidiid clams (family Pisidiidae formerly Sphaeriidae-ICZN Declaration 27). This family of freshwater clams is represented in North America by three major genera, *Pisidium, Musculium* and *Sphaerium*. All of these forms are quite small (generally $<$ 20 mm) with species of the genus *Pisidium* usually containing the smallest individuals ($<$10 mm) and the genus *Sphaerium* containing the largest (Burch, 1975). These clams have a worldwide distribution (Burch, 1975) and are important components of many freshwater systems (Avolizi, 1976; Alexander, 1978; Hornbach et al., 1984) Burky (1983) has reviewed the general physiological ecology of this group. His review contains information on metabolism in these forms but is relatively restricted in scope. In this paper I will examine published reports on the metabolic rates of pisidiid clams and attempt to identify general trends making intergeneric comparisons where possible. In addition new metabolic data is given for two populations of *Pisidium casertanum* and compared with published values to demonstrate the degree of intraspecific variation in metabolism and its potential relationship to life history traits.

ENVIRONMENTAL INFLUENCES ON METABOLISM

Very few studies have dealt specifically with elucidating the major factors which affect the rate of metabolism in pisidiid clams. There are however a number of studies which have assessed metabolic rates under various conditions as a part of a larger study. The most common is where benthic metabolism is being calculated for a given habitat and pisidiids happen to be a member of the particular benthic community (e.g. Johnson and Brinkhurst, 1971a,b; Mason, 1977). Still other studies have examined metabolism as a component of the overall energy budget for populations of pisidiid clams (e.g. Holopainen, 1978; Alexander, 1982; Hornbach et al., 1983, 1984a,b; Way, 1983). Table 1 lists the species of pisidiids for which data on metabolism could be obtained. A great variety of techniques have been utilized to assess metabolic rates in these forms which adds considerably to the variation in reported rates. Despite this variability some general trends in metabolism can be noted. For a discussion of the factors which affect the rate of metabolism I will concentrate on the effects of body size, temperature and season, and oxygen availability. I will conclude this overview by examining the possible influences of these factors on the population energetics of these forms.

BODY SIZE

The metabolic rate of an organism can be related to weight by the familiar exponential equation $\mathring{V}_{O_2} = aW^b$, where $\mathring{V}_{O_2}$ is the metabolic rate (volume of O_2 consumed per individual per unit time), W is the weight and a and b are constants. The value of a is related to the absolute level of metabolism and the value of b describes how metabolism varies with size. Values of b $<$1 indicate that metabolic rates increase with weight but larger individuals have lower WEIGHT-SPECIFIC metabolic rates than small individuals. A general value of 0.75 is often assigned to b (Prosser, 1973) however Phillipson (1981) gives b-values ranging from 0.66–1.14 for multicellular ectotherms with an overall b-value of 0.88 for these forms. Alimov (1975) is of the opinion that a generalized b-value of 0.90 is representative of the Pisidiidae. Table 2 shows that b-values exhibit both intra- and inter-specific variability in the pisidiids, with values ranging from 0 (metabolic rate constant regardless of weight) to 1.24. For most populations the upper limit for b-values is near 1, indicating that absolute metabolic rate increases proportionately with size, i.e. weight-specific metabolic rate is a constant. Burky and Burky (1976) claimed a b-value of 1.0 in *Pisidium walkeri* (exhibited over a wide range of temperature and season) and indicated that this may have been due to the small size range of clams and due to the fact that these clams contained developing embryos (pisidiids are viviparous) that would be metabolizing at high weight-specific rates. The studies of Way et al. (1981) on *Musculium partumeium*, and Collins (1967) on *Sphaerium occidentale* have also shown b-values of 1 under a variety of conditions. The studies of Holopainen and Ranta (1977b) have shown that b-values increased as temperature increased for *P. casertanum* and *P. henslowanum,* while the b-value for *P. conventus* decreased with increasing temperature. They correlated this difference with the fact that *P. conventus* is a profundal (and thus a cold stenotherm) species whereas the other two species are found in the littoral zones and are eurythermic. While the number of seasonal studies on metabolism in the pisidiids is limited (Table 2) they show that temperature alone does not explain changes in b-value. The studies of Way and Wissing (1984) on *P. compressum* and *P. variabile* and Alexander (1982) on *M. lacustre* have shown that b-values are highest during reproduction, with values near or exceeding 1. This indicates that reproductively active adults have weight-specific metabolic rates equalling or surpassing those of smaller individuals. Again this could be partially due to the presence of incubating larvae or could represent an overall increase in metabolism (including feeding) during periods of reproduction. Hornbach et al. (1983) however, have found that b-values were low during peak periods of reproduction in *S. striatinum.* In addition, they found that during these periods, weight-specific feeding rates

Table 1. List of populations referred to in this review on the metabolism of pisidiid clams.

Genus	Species	Population Reference Number	Graph Symbol in Fig. 1	Reference
Musculium				
	lacustre	1	1	Wesenmeier, 1960
	lacustre	2	2	Alexander, 1982; Buchwalder, 1983
	partumeium[a]	3	3	Hornbach, 1976; Way et al., 1981
	partumeium[b]	4	4	Way, 1978; Way et al., 1981; Buchwalder, 1983
	partumeium	5	5	Hornbach, 1983
	securis	6	6	McKee and Mackie, 1983
Pisidium				
	amnicum	7	A	Holopainen and Ranta, 1977a
	casertanum	8	B	Berg et al., 1962; Berg and Jonasson, 1965; Jonasson, 1972; Holopainen and Jonasson, 1983
	casertanum	9	C	Johnson and Brinkhurst, 1971a,b
	casertanum	10	D	Holopainen and Ranta, 1977b; Holopainen, 1978
	casertanum	11	E	Mason, 1977
	casertanum[c]	12	F	this study
	casertanum[d]	13	G	this study
	compressum	14	H	Johnson and Brinkhurst, 1971a,b
	compressum	15	I	Way and Wissing, 1984
	conventus	16	J	Holopainen and Ranta, 1977b
	henslowanum	17	K	Johnson and Brinkhurst, 1971
	henslowanum	18	L	Holopainen and Ranta, 1977b
	nitidum	19	M	Alimov, 1975
	obtusale	20	N	Bleck and Heitkamp, 1980
	personatum	21	O	Bleck and Heitkamp, 1980
	variabile	22	P	Way, 1984
	ventricosum	23	Q	Johnson and Brinkhurst, 1971
	walkeri	24	R	Burky and Burky, 1976
Sphaerium				
	corneum[e]	25	a	Alimov, 1965
	corneum[f]	26	b	Alimov, 1965
	corneum	27	c	Arabina and Rubinova, 1971 (in Alimov, 1975)
	corneum	28	d	Kovaleva, 1970 (in Alimov, 1975)
	occidentale	29	e	Collins, 1967
	occidentale	30	f	McKee and Mackie, 1983
	rivicola	31	g	Alimov, 1975
	rivicola	32	h	Kondrat'ev, 1970 (in Alimov, 1975)
	rivicola	33	i	Kovaleva, 1970 (in Alimov, 1975)
	scaldianum	34	j	Alimov, 1975
	simile	35	k	Waite and Neufeld, 1977
	solidum	36	l	Kovaleva, 1970 (in Alimov, 1975)
	striatinum	37	m	Hornbach et al., 1983

[a] Drew Woods population
[b] Aullwood Marsh population
[c] Farrier's Pond population
[d] Riopel Pond population
[e] Udel'nyi Park population
[f] Old Petergof population

were high for large clams and concluded that the reduction of weight-specific metabolism coupled with this high rate of feeding allowed large clams to allocate greater amounts of energy to reproduction due to this metabolic economy.

Much of the intra- and inter-specific variation in b-values can be attributed to seasonal and/or temperature variation. In order to compare b-values across genera it is necessary to control, as much as possible, these confound-

Table 2. List of various types of metabolic data available for pisidiid clams. Valves of b refers to the weight exponent in the equation $\mathring{V}_{O_2} = aW^b$ and Precht acclimation types are after Precht, 1958.

Genus	Species	Population Reference[1]	Seasonal data ?	Date at low O_2 ?	Date in air ?	b-values	Q_{10}-Overall	Q_{10}-Summer acclimated (≥20°C)	$Q_1$0-Winter acclimated (≤10°C)	Precht type
Musculium	*lacustre*	1	—	—	—	0.94	—	—	—	—
	lacustre	2	yes	yes	—	0.44–1.34	0.4– 5.9	0.67–5.88	0.65–3.16	—
	partumeium	3	yes	yes	—	1.00	0.3– 1.4	0.27–1.41	0.55–1.06	I
	partumeium	4	yes	—	—	1.00	0.4– 2.7	0.39–1.66	1.17–2.49	I,II,III,IV,V[b]
	partumeium	5	—	—	—	0.50–1.17	0.7– 8.3	1.00–7.60	0.70–8.30	I
	securis	6	yes	—	—	—	0.7– 2.5	1.90–2.50	0.70–1.70	IV[c]
Pisidium	*amnicum*	7	—	—	—	0.58–0.88	1.5– 5.6	—	1.50–9.66	I[c]
	casertanum	8	—	yes	—	—	0.8–12.3	—	0.80–12.30	—
	casertanum	9	—	—	—	0.31–1.00	4.8– 9.8	—	—	—
	casertanum	10	—	—	—	0.66–0.82	2.1–14.8	—	2.12–14.76	—
	casertanum	11	—	—	—	0.12–0.19	0.7– 0.9	—	0.69–0.85	—
	casertanum	12	—	—	—	0.36–1.05	0.3–11.9	0.32–0.91	11.87	—
	casertanum	13	—	—	—	0.44–1.11	0.2– 5.3	1.39–5.26	0.18	—
	compressum	14	—	—	—	0.00–0.85	1.7– 5.4	—	—	—
	compressum	15	yes	—	—	0.21–0.99	—	—	—	—
	conventus	16	—	—	—	0.58–1.05	1.0–12.8	—	1.96–12.75	—
	henslowanum	17	—	—	—	0.61–1.00	3.8– 6.1	—	—	—
	henslowanum	18	—	—	—	0.71–0.83	2.4– 3.3	—	2.38–3.29	—
	nitidum	19	—	—	—	—	—	—	—	—
	obtusale	20	—	—	yes	—	1.9– 2.8	2.05–2.42	1.86–1.96	—
	personatum	21	—	—	yes	—	0.7– 5.9	0.67–5.86	2.48	—
	variabile	22	yes	—	—	0.35–0.97	—	—	—	—
	ventricosum	23	—	—	—	0.40–0.96	4.9– 6.9	—	—	—
	walkeri	24	yes	—	—	1.00	0.7– 2.8	1.51–2.78	0.67–1.69	I,V
Sphaerium	*corneum*	25	yes	—	—	0.12–1.24	—	—	—	V[c]
	corneum	26	yes	—	—	0.32–0.52	—	—	—	V[c]
	corneum	27	—	—	—	1.01	—	—	—	—
	corneum	28	—	—	—	1.13	0.8– 7.3	0.83–1.74	2.25–7.29	—
	occidentale	29	—	—	yes	0.62–1.06	1.5– 2.7	1.96–2.41	—	—
	occidentale	30	yes	—	—	1.00	—	—	—	I,V[b]
	rivicola	31	—	—	—	0.90	—	—	—	—
	rivicola	32	—	—	—	0.74	—	—	—	—
	rivicola	33	—	—	—	—	2.2– 2.3	—	2.21–2.25	—
	scaldianum	34	—	—	—	—	—	—	—	—
	simile	35	—	yes	—	—	1.3– 2.2	1.32–2.21	—	—
	solidum	36	—	—	—	—	0.8– 3.5	0.79–1.12	1.34–3.49	—
	striatinum	37	yes	—	—	0.53– 1.45	0.2– 7.2	0.21–2.40	1.46–7.20	—

[a] See Table 1

[b] Varies with size and temperature

[c] Type suggested by limited data; not explicitly stated by author

ing factors. In an attempt to examine intergeneric differences in b-value, I obtained all the values of oxygen consumption for as many size classes of as many species of pisidiids that were available in the literature for 20°C acclimated animals at 20°C. All values were converted to $\mu lO_2 \cdot clam^{-1} \cdot hr^{-1}$ using conversions of 1.429 mgO_2/mlO_2 and a respiratory quotient of 0.812 (Russell-Hunter et al., 1968) for converting mass values to volume value and for converting CO_2 production (as a measure of metabolism) to O_2 consumption. All weights were converted to ash free dry tissue weight values (published values of total dry weight: tissue dry weight were obtained from many sources; especially valuable is the paper by Mackie and Flippance, 1983). Figure 1 shows the 337 values obtained (114 for *Pisidium,* 69 for *Musculium* and 154 for

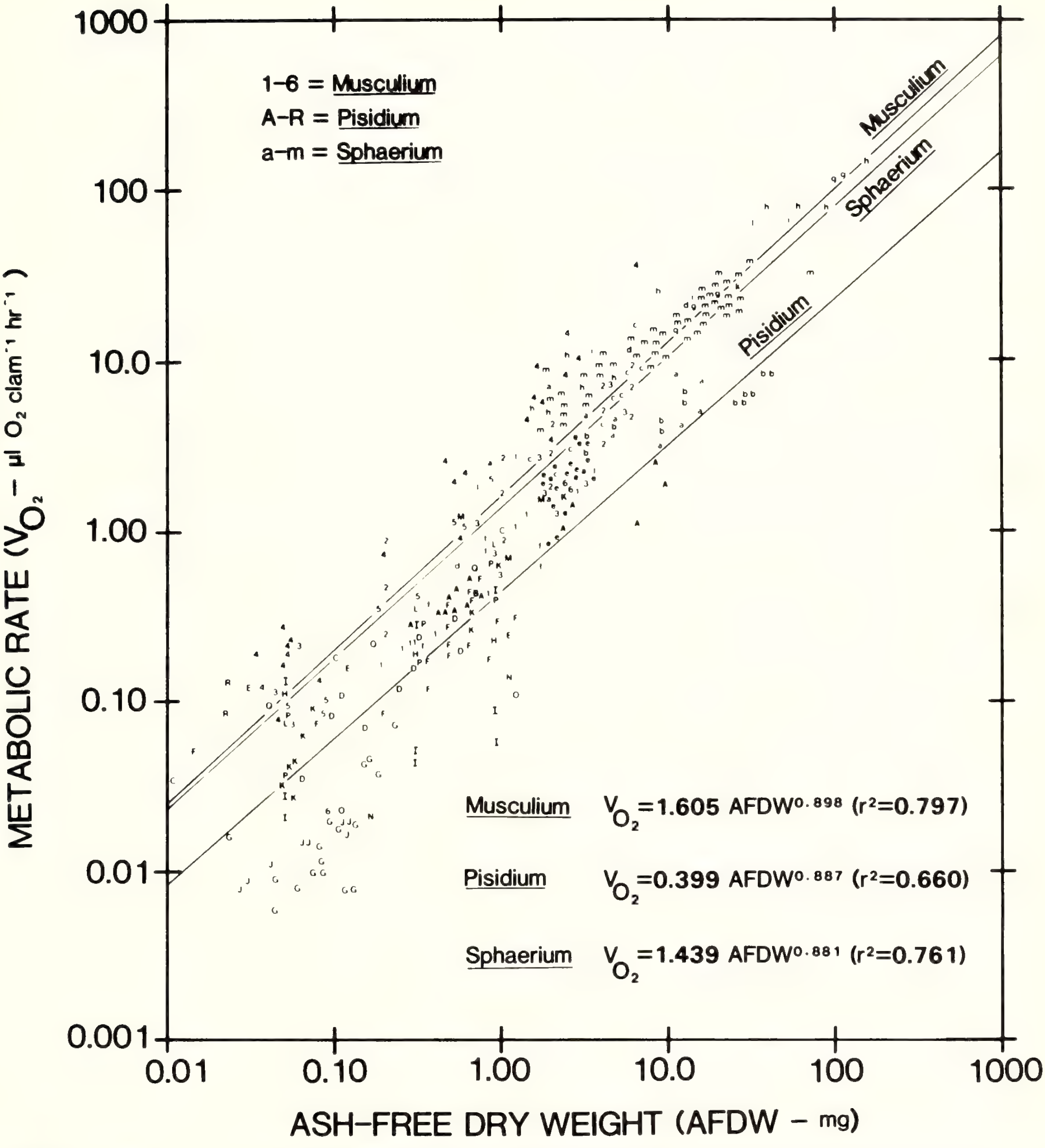

Fig. 1. Relationship between body size (ash-free dry weight) and metabolic rate at 20°C for 37 populations of pisidiid clams. Symbols 1–6, A-R and a-m are for populations of *Musculium, Pisidium* and *Sphaerium* respectively. References for the particular populations are given in Table 1. Regression lines and equations are also given.

Sphaerium). Regression analyses on log transformed data resulted in the following relationships between ash free dry weight (AFDW-mg) and metabolic rate ($\mathring{V}_{O_2}$-μlO$_2$·clam^{-1}·hr^{-1}): $\mathring{V}_{O_2}=0.399\text{AFDW}^{0.887}$ ($r^2=0.660$) for *Pisidium;* $\mathring{V}_{O_2}=1.439\text{AFDW}^{0.881}$ ($r^2=0.761$) for *Sphaerium;* and $\mathring{V}_{O2}$ = 1.605 AFDW$^{0.898}$ (r^2 = 0.797) for *Musculium.* The b-values (0.887, 0.881, 0.898) were not significantly different from one another (analysis of covariance; F for slopes = 0.025, 2,331 df, Prob. F>.50) (Zar, 1974). A common b-value of 0.89 (SE = 0.030) can be used to represent the effect of size on metabolic rate for these three groups. It should be noted that this value only applies at 20°C and across taxa. It should not be used to calculate specific rates within species. This common value does however tend to indicate that there is no intergeneric differences in the overall way in which metabolic rate is influenced by weight. This value of 0.89 is significantly different from 1.0 (t = 3.73, 333 df, prob. t < .001) indicating that larger clams within a genus have lower weight-specific metabolic rate than smaller clams in that genus. This value of 0.89 is not significantly different (t = .071, 382df, prob. t >.50) from the value of 0.90 reported by Alimov (1975) based on 47 values of metabolic rate at 20°C for the three genera.

Animal size then seems to affect metabolic rate in a consistent fashion across species, within and between genera in the pisidiids at least 20°C. However, as noted above, there is considerable seasonal variation in the relationship between weight and metabolic rate in this group. Additional seasonal studies, which include data on specific life-histories are needed to allow for a more complete interpretation of seasonal trends in weight-rate relationships.

THE EFFECT OF TEMPERATURE AND SEASON

Generally increasing temperatures are assumed to cause an increase in metabolic rates in ectothermic animals. One index of the magnitude of this effect is Q_{10}, the rate at which metabolic rate increases for a 10°C increase in temperature. Q_{10}'s are often in the range of 2 to 3 indicating that as temperature increases 10°C metabolic rates double or triple. The ranges of Q_{10}-values reported for pisidiids are given in Table 2. There is a large variance in ranges from 0.2 to 14.8. Q_{10}-values less than 1.0 indicate that as temperature increases metabolic rates decrease (see Burky 1983 for a discussion of the ecological significance of this phenomenon often termed "respiratory impairment"). There were no significant differences found between genera in either the lower range of Q_{10}-values reported (Kruskal-Wallis, $H_c = 5.46$, 0.10>prob. H_c>0.05) or the upper range of Q_{10}-values ($H_c = 2.78$, 0.25>prob H_c>0.10).

There are a number of underlying factors which add to the variability in Q_{10}-values reported. Q_{10} can vary with body size, temperature and season. Hornbach (1983) has shown that over the temperature range 5–10°C, Q_{10}-values are 0.27, 2.71 and 5.15 for *M. partumeium* of weight 0.03, 0.30 and 3.00 mg respectively. Studies by Alexander (1982) and Hornbach et al. (1983) have also shown that Q_{10} varies with size but that the relationship between Q_{10} and size differs with season. For example, in *S. striatinum* (Hornbach et al., 1983) small clams have higher Q_{10}s in the winter but lower Q_{10}s in the summer than large clams. In an attempt to identify general patterns of seasonal influences on Q_{10}, values were compiled for summer (≥20°C) and winter acclimated (≤10°C) animals (Table 2). There was no significant difference in either the lower end of the range of Q_{10} values (paired Wilcoxon, T = 22, n = 11, 0.5>prob. T>0.2) or at the higher end of the Q_{10} range (T = 22, n = 11, 0.5>prob. T>0.2) for summer vs. winter acclimated animals. Thus no general seasonal trends in Q_{10} variation or differences between genera can be discerned.

As might be expected from the discussion above on the great variability of Q_{10}-values and the lack of seasonal trends in Q_{10}, a variety of acclimation patterns have been demonstrated for the pisidiids. Acclimation refers to the fact that while Q_{10}-values are generally > 1 for short term temperature increases, if an organism is maintained at a new temperature for a period of days or weeks the metabolic rate function may compensate. Major patterns of acclimation have been identified and are often referred to as Precht acclimation types (Prosser, 1973). In the pisidiids the most common acclimation type appears to be a Precht Type I (Table 2). This is a pattern of overcompensation, i.e. warm acclimated animals have lower metabolic rates (at their acclimation temperature) than cold acclimated clams (at their acclimation temperature). McKee and Mackie (1983) interpret Type I patterns as adaptive for it allows cold adapted animals to quickly respond to increasing temperatures (cold acclimated animals which display Type I acclimation would have higher metabolic rates than warm acclimated animals at equivalent temperatures), and they claim that this is especially important in the spring when pisidiids are entering a period of intense growth and reproduction. Burky and Burky (1976) claim that the Type I pattern is adaptive for it implies that since warm acclimated animals have lower metabolic rates they can be more efficient in partitioning energy to growth and reproduction which normally occurs during the warmer summer months. Another common acclimation type found in the pisidiids is a Precht Type V, reverse or "paradoxical" compensation. A Type V pattern indicates that warm acclimated animals have higher metabolic rates than cold acclimated animals when measured at equivalent temperatures and may represent an energy conservation mechanism during periods (e.g. winter) when high levels of activity would not be productive in obtaining resources for growth (i.e. resources are limiting). McKee and Mackie (1983) clainmed that a Type V pattern displayed by medium sized *S. occidentale* over the period from April to July allowed warm acclimated clams to maintain higher metabolic rates and thus have increased exploitation of available energy during times of optimal growth. Burky and Burky (1976) also claim that a Type V pattern displayed by the summer generation of *P. walkeri* in a small pond allows these forms to efficiently exploit available energy sources. Hornbach (1983 and unpublished data) has shown that acclimation patterns can differ with temperature and size for *M. partumieum.* Over the range of 10–15°C a Type V pattern was noted for all sizes of clams while at lower temperatures (5–10°C) acclimation pattern was dependant on size. Small clams displayed a Type I pattern while large clams displayed Type V pattern. All of the authors that have dealt extensively with acclimation patterns in pisidiid clams point out that no one pattern of acclimation applies to a specific population of clams and that patterns shift and change with size and season to allow these animals to most efficiently exploit prevailing physical and biological conditions (Burky and Burky, 1976; Alexander, 1982; Hornbach, 1983; McKee and Mackie, 1983) (see also discussions in Burky 1983).

EFFECTS OF OXYGEN AVAILABILITY

It has long been known that pisidiid clams are able to survive in anaerobic environments (Juday, 1908). Despite this fact there are few studies which have considered the influence of 0_2 availability on metabolism in this group (see Table 2). Both Waite and Neufeld (1977) and Berg et al. (1962) found a relatively broad range of oxygen independence for *S. simile* and *P. casertanum,* respectively. Metabolic rates decreased with falling 0_2 levels only at low concentrations of oxygen. Buchwalder (1983) found that for *M. partumeium* and *M. lacustre* there is a dependence of metabolic rate on 0_2 availability over a broad range of 0_2 concentrations. In fact, Buchwalder found that the dependence of metabolism on 0_2 level varied seasonally and the greatest independence was found during times of lowest 0_2 availability. In fact many pisidiids grow and reproduce under low 0_2 conditions. This is true for both *M. partumeium* (Thomas, 1963, 1965; Way et al., 1980) and *M. lacustre* (Alexander, 1982), and may be true for species which inhabit the profundal zones of lakes (see e.g. Berg et al., 1962) or the anoxic sediments in eutrophic lakes and ponds.

Hochachka (1980) has reviewed the major anaerobic biochemical pathways utilized by molluscs. Though no study to date has dealt exclusively with this problem in pisidiids there are indications that these forms utilize some of the alternative metabolic pathways which allow efficient anaerobic metabolism. For example Hornbach et al. (1980b) have shown that several species of *Sphaerium* have the anaerobic enzyme malate dehydrogenase. This enzyme is also found in *Musculium partumeium* and *Musculium securis* (Hornbach et al. 1980a) and in *Pisidium casertanum* (personal observation), *P. variabile* and *P. compressum* (G. L. Mackie, personal communication). C. M. Way (personal communication) has also detected the presence of octopine dehydrogenase, another anaerobic enzyme, in *Sphaerium striatinum.* While the exact nature of the biochemical pathways involved in the anaerobic metabolism of the pisidiids still needs to be elucidated, it is clear that metabolism at low 0_2 levels is of extreme importance in this group.

THE ENERGETICS OF METABOLISM

As mentioned in the introduction, the energy partitioned to metabolism often accounts for the largest percentage of assimilated energy. The amount remaining can be partitioned to growth and reproduction, i.e. production. The production efficiency for pisidiid clams (i.e. production:assimilation ratio) ranges from 10 to 79%, (Table 3) thus energy partitioned to metabolism accounts for 31 to 90% of assimilation in these forms. There is no significant difference in the production-to-assimilation ratios between genera (Kruskal-Wallis, $H_c = 0.26$, $0.9 > \text{prob. } H_c > 0.75$). Thus while production efficiencies vary in this family there are no intergeneric differences. This is not to imply however that there are no intergeneric differences in metabolism in the Pisiidae. Refering back to figure 1, there were no differences in how size affected metabolic between genera (i.e. no differences in b-values from $\mathring{V}_{O_2} = aW^b$ at 20°C). There are however significant differences in a-values (analysis of covariance, F for elevations = 83.3, 2,333 df, prob. F. < 0.001). The a-values are 0.399, 1.605 and 1.439 for *Pisidium, Musculium* and *Sphaerium* respectively. Student-Newman-Keuls multiple range tests indicates that the a-value for *Pisidium* is significantly lower than those of *Musculium* and *Sphaerium*, but that the a-values for the latter two genera are not significantly different from one another.

This lowered metabolic rate for *Pisidium* is quite interesting for if individuals of the genus *Pisidium* had both the same a and b-values as *Musculium* and *Sphaerium* their weight-specific rates would be higher because of their much smaller size. However with the lowered a-value small individuals of *Pisidium* can have lowered weight-specific rates. For example an average sized *Musculium* and *Sphaerium* (0.52 and 6.27 mg ash free dry weight respectively) have metabolic rates of 1.73 and 1.17 $\mu l0_2 \cdot mg\ weight^{-1} \cdot hr^{-1}$ respectively, based on a-values given above and a common b-value of 0.89. If a 0.24 mg *Pisidium* individual had an a-value of 1.5 then an average sized Pisidium would have a rate of 1.76 $\mu l0_2 \cdot mg\ weight \cdot hr^{-1}$. Instead the lowered a-value (0.399) means that it would have a weight-specific rate of only 0.47 $\mu l0_2 \cdot mg^{-1} \cdot hr^{-1}$, approximately one-third that of an average sized *Musculium* of *Sphaerium.* This lowered weight-specific rate is interesting in light of the fact that members of the genus *Pisidium* generally have reduced gills when compared to the other two genera (Odhner, 1929). This reduction in respiratory surface could be, at least in part, an evolutionary response to a reduction in metabolic demands. However, bivalve gills generally have a larger surface area than required for gas exchange since the gills are used in filter-feeding (Russell-Hunter, 1979) and this reduction may be a response to deposit-feeding in members of the genus *Pisidium* (Meier-Brook, 1969).

The lowered metabolic rates found in the genus *Pisidium* does not however mean that they are metabolically more efficient than the other genera. As noted above there is no difference in production efficiencies among the three genera. One would predict then, that since members of the genus *Pisidium* have lower weight-specific metabolic rates than the other two genera, and since the proportion of assimilation that they partition to metabolism is similar to the other two genera, they should have lower rates of production per unit weight. One measure of production per unit weight is the production-to-biomass ratio (P:B). The annual P:B ratios for various species of pisidiid clams are given in Table 3 (see Hornbach et al., 1984 for methods of calculation). There are significant differences in P:B values between genera (Kruskal-Wallis, $H_c = 8.79$, 2 df, $.025 > \text{prob. } H_c > .01$) with val-

Table 3. Values of annual production-to-biomass ratio (P:B), and net production efficiency (P:A) for various pisidiid clams.

Species	P:B	100 × (P:A)	Reference	Population Reference Number[a]
Musculium lacustre	7.7–8.0[b]	10–15[b]	Alexander, 1982	2
Musculium partumeium	11.4	45–48[b]	Burky, 1983	4
Musculium partumeium	7.2	62	Burky, 1983	3
Musculium securis	2.2	—	Qadri et al., 1974	—
Pisidium amnicum	1.4	—	Vincent et al., 1981	—
Pisidium casertanum	3.8	—	Hamill et al., 1979	—
Pisidium casertanum	1.3	53	Holopainen, 1978	10
Pisidium casertanum	0.8–1.1[d]	—	Holopainen and Jonasson, 1983	10
Pisidium casertanum	2.9–6.0[e]	—	Mackie et al., 1983	—
Pisidium casertanum	0.5–10[d]	40–42[d]	Mason, 1977	11
Pisidium casertanum	0.2	24	Jonasson, 1972	8
Pisidium compressum	4.3	—	Gillespie, 1969	—
Pisidium compressum	3.9	67	Way, 1983	15
Pisidium conventus	1.0	79	Holopainen and Hanski, 1979	16
Pisidium crassum	1.3	29	Alimov, 1970	—
Pisidium crassum	2.2	28	Alimov, 1981	—
Pisidium dubium	—	47	Teal, 1957	—
Pisidium ferrugineum	2.0–5.9[e]	—	Mackie, et al., 1983	—
Pisidium lilljeborgi	1.2	26	Alimov, 1981	—
Pisidium nitidium	0.8	—	Alimov, 1981	19
Pisidium subtruncatum	0.8–1.2[a]	—	Holopainen and Jonasson, 1983	—
Pisidium variable	3.4	29	Way, 1983	22
Pisidium sp.	1.2–1.5[c]	20	Johnson and Brinkhurst, 1971a,b	9,17,23
Pisidium sp.	—	—	Lindegaard and Jonasson, 1979	—
Pisidium sp.	2.2	15	Tudorancea et al., 1979	—
Sphaerium corneum	0.4	—	Arabina, 1966	—
Sphaerium corneum	3.5	—	Mann, 1971	—
Sphaerium suecicum	1.5	44	Alimov, 1970	—
Sphaerium simile	3.0	—	Avolizi, 1970, 1976	—
Sphaerium striatinum	4.5	—	Avolizi, 1970, 1976	—
Sphaerium striatinum	4.6	44	Hornbach, et al., 1948b	37

[a] see Table 1
[b] range for 2 generations
[c] range for various sampling stations
[d] range for various years
[e] range for populations

ues of P:B averaging 2.44, 2.92, and 7.30 for *Pisidium Sphaerium* and *Musculium*, respectively. Thus, as predicted, the genus *Pisidium* does display a lower P:B than the other two genera, but it is not significantly lower than the ratio for the genus *Sphaerium.* The higher P:B ratio for *Musculium* may be attributable to adaptations for life in ephemeral habitats and shorter life-spans (usually 1 yr) (Way et al., 1980).

The overall lower rate of weight-specific metabolism and lower weight-specific production may have far reaching effects for the genus *Pisidium*. For example, it is known that the reproductive habits of members of the genus *Pisidium* differs from that of the other two genera. Pisidiids are viviparous (ovoviviparous—Mackie, 1978) and species of *Musculium* and *Sphaerium* may carry a number of different ontogenetic states of young in their gills at any one time. Individuals of the genus *Pisidium*, however can only brood one ontogenetic stage at a time. This might partially be due to restricted space because of their small size but it might also be indicative of these forms inability to support a large reproductive energy drain because of their lowered weight-specific metabolism and production.

There are very few studies that accurately assess complete energy budgets for pisidiid clams which include measures of energy partitioned to metabolism (see Burky, 1983). Certainly more studies are needed so that the strategies involved in optimizing energy to metabolism can be identified. Intra-specific studies are needed which allow for the examination of environmental influences on this partitioning within a group that has a relatively similar homogenous genetic makeup.

INTRASPECIFIC VARIATION IN METABOLISM AND ITS RELATIONSHIP TO LIFE-HISTORY TRAITS: AN EXAMPLE OF *PISIDIUM CASERTANUM*

It should be clear from the above discussion that there is a great deal of variability in the patterns of metabolism in the pisidiids. There is very little systematic variation in Q_{10}-values, b-values from the weight-rate relationships or in the amount of assimilated energy partitioned to metabolism. One of the major reasons that general trends are difficult to discern is due to the great deal of intraspecific variability in metabolism. A large portion of this variability allows particular populations within a species to have local adaptions to varying environments (see discussion in Russell-Hunter, 1978 concerning the short term transient nature of freshwater habitats and the role of phenotypic plasticity in adapting to these environments). In this section I will provide new metabolic data for two populations of *Pisidium casertanum* and will compare these to published results. The major emphasis will be to show how the intraspecific variation noted can have a great influence on the range of life histories within this species.

NEW DATA

Clams for this study were collected from two ponds in southwest Virginia (details in Cox and Hornbach, 1983). One pond (Riopel pond-RP) is located at an altitude of 1164 m. The water in this pond is ion-poor having an average conductivity of about 15 μmhos·cm^{-1}. The *P. casertanum* from this pond are generally less than 3 mm in shell length. The other pond from which clams were collected (Farrier's pond-FP) is located at an altitude of 595 m and has water with a much higher ion content that RP (conductivity of FP approximately 250 μmhos·cm^{-1}). The clams from FP are larger than those in RP, many exceeding 4 mm.

Clams were collected in July or August and March for determination of metabolic rates. Clams were allowed to habituate for 24 hours prior to determination of metabolic rates. Metabolic rates (as 0_2 consumed) were determined by a closed bottle technique described by Hornbach, et al. (1983). This method involves placing 10–30 clams (depending on size), in 40-ml ground glass dropper bottles containing filtered (0.45μm) pondwater. The difference in the 0_2 content of control (bottles with no clams) and experimental chambers (determined by Winkler titration) provided a measure of the amount of 0_2 consumed. Generally experiments were conducted for 12–24 hrs (depending on temperature) and clams consumed less than 10% of the available oxygen.

For winter acclimated (March) clams metabolic rates were determined at 5° and 10°C, while for summer acclimated (July-August) clams metabolic rates were determined at 20°, 25° and 30° C (The temperatures were maintained at ± 1°C in water baths). Figure 2 presents all of the metabolic rates measured for the two populations. Table 4 gives the a and b-values from the equation $\mathring{V}_{O_2} = aAFDW^b$ (where $\mathring{V}_{O_2} = \mu l0_2$ consumed·clam^{-1}·hr^{-1} and AFDW = ash free dry weight in mg) for each temperature at which metabolic rates were determined. At any temperature there was no significant difference in b-values between populations (analyses of covariance). There were however significant differences in b-values between temperatures. Generally b-values were greater for winter acclimated animals than for summer acclimated animals. This is similar to the results found for *P. casertanum* by Holopainen and Ranta (1977b). Again this indicates that body size has a much greater influence on the metabolic rates of summer acclimated animals than on winter acclimated clams. For example a 1.0 mg clam from RP whose $\mathring{V}_{O_2}$ was measured at 10°C had a weight-specific metabolic rate of approximately 1.5 times that of a 0.01 mg clam, whereas at 20°C a 1 mg clam from RP would have a weight-specific metabolic rate 2.6 times that of a 0.01 mg clam.

The b-values of 0.82 and 0.50 for the RP and FP populations at 20° respectively (Table 4) are not significantly different (analysis of covariance F = 1.63, 1,29 df prob F>0.20) and thus a common b-value (Zar, 1974) of 0.57 can be assigned to these 2 populations at 20°C. This value is not significantly different (t=0.546, 366 df, prob t>0.50) than the value at 0.89 that was derived for all pisidiids at 20°C (see Fig 1 and discussion of the effect of body size on metabolic rate above).

Despite the fact that there were no difference in b-values between populations within temperatures there were differences in a-values (analyses of covariance) at 10°, 20° and 25°C. This implies that at these temperatures there were differences in metabolic rates between clams collected from the two ponds but the manner in which metabolic rate varied with size was the same between the two populations. Since both a and b-values vary with temperature, Q_{10}-values vary with temperature and body size. This is common among the pisidiids (see the discussion of the effects of temperature and season on metabolic rates above). Values of a, vary much less for the RP population than for the FP population (Table 4). This indicates that temperature has a much greater effect on the FP population. Apparently the RP population clams generally maintain a fairly constant but low level of metabolism.

Examining a-values for summer and winter acclimated animals determined at their acclimation temperature (a=0.156 and 0.102 for winter (5°C) and summer (26°C) acclimated clams from RP and a = 0.417 and 0.273 for winter (10°C) and summer (28°C) acclimated clams from FP—Table 4) indicate that *P. casertanum* from these ponds may

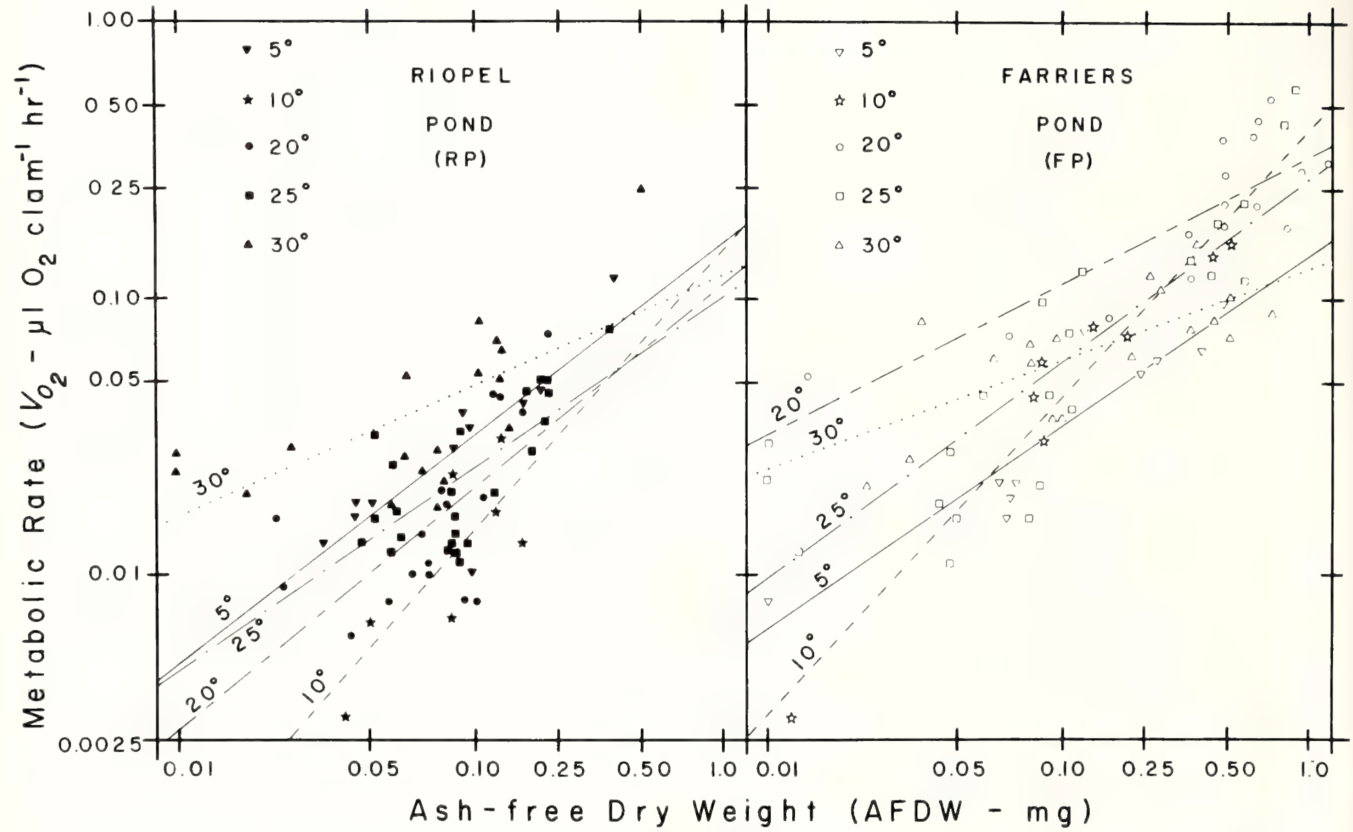

Fig. 2. Relationship between body size (ash-free dry weight) and metabolic rate of *Pisidium casertanum* from 2 ponds in southwest Virginia. Rates were determined at 5 temperatures and regression lines are shown for each temperature.

Table 4. Values of ln(a), a, b from the equations $\ln(\mathring{V}_{O_2}) = \ln(a) + b \ln(AFDW)$ and $\mathring{V}_{O_2} = a\, AFDW^b$ for two populations of *Pisidium casertanum* (Riopel Pond-RP and Farriers Pond-FP) from southwest Virginia. Values of r^2 and F, from linear regressions of ln(AFDW) on $\ln(V_{O2})$ and values of n (total # of clams) and N (total number of test chambers) for the regression analyses.

Date collected	Temperature at which collected	Population	Temperature at which $\mathring{V}_{O_2}$ determined	ln(a)	a	b	r^2	F	n	N
4 Mar 83	5°	RP	5°	−1.855	0.156	0.762	0.679	19.00**	302	11
4 Mar 83	5°	RP	10°	−1.905	0.149	1.112	0.620	8.14*	229	7
1 Jul 82	22°	RP	20°	−2.168	0.114	0.818	0.413	10.54**	445	17
23 Jul 82	26°	RP	25°	−2.285	0.102	0.709	0.481	20.43**	599	24
10 Aug 82	23°	RP	30°	−2.127	0.119	0.438	0.433	12.23**	421	18
4 Mar 83	10°	FP	5°	−1.936	0.144	0.682	0.864	50.71**	174	10
4 Mar 83	10°	FP	10°	−0.875	0.417	1.054	0.949	111.82**	273	8
20 Jun 82	27°	FP	20°	−1.101	0.333	0.502	0.670	28.38**	259	16
1 Jul 82	28°	FP	25°	−1.297	0.273	0.725	0.711	49.31**	464	22
2 Aug 82	25°	FP	30°	−2.047	0.129	0.364	0.510	16.65**	389	18

*significant at 0.05 level
**significant at 0.01 level

display a Precht Type I pattern of overcompensation. As mentioned above (The Effect of Temperature and Season, and Table 2) this is the most common acclimation pattern displayed by pisidiids.

In addition to the values given above, there are additional values of metabolic rate available for *P. casertanum* (see Table 2). Of these other studies only those of Berg and Jonasson (1965) and Holopainen and Ranta (1977b) are on populations for which additional information on the habitat and populations are available. In Table 5, I have given values of metabolic rate for small (0.01 mg AFDW), medium (0.10 mg) and large (1.00 mg) clams at various temperatures. *P. casertanum* from Riopel pond generally have lower metabolic rates than clams from other populations. This is especially apparent for temperatures of 20° and 25°C. For example at 20°C, 0.01 mg clams from Farrier's pond have metabolic rates 11 times those of the same sized clams from Riopel pond. It is at these warmer temperatures when the major growth and reproduction takes place in these populations, thus it is quite significant that clams from RP have lower metabolic rates. Table 6 shows that the clams from Riopel pond reach a much smaller maximum adult size than clams from other populations and they have a lower maximum number of embryos per adult. Thus it appears that the lowered metabolism in this population is reflected in a number of life history parameters. Clams from RP probably do not have higher production efficiency (P:A) or reproductive effort (Re:P) than clams for RP, for if they did, this would be exhibited in growth and reproductive output more near that of clams from FP.

The cause for this lowered metabolism in clams from RP is unknown. It may be the lowered Ca content of the water in Riopel Pond as compared to the other populations (Table 6) restricts growth. It is also possible that food resources are more restricted in RP which result in lowered ingestion rates and thus lowered overall metabolic rates. Preliminary results from transfer experiments between FP and RP and from laboratory studies where food and Ca availability are controlled (Cox and Hornbach, 1983 and unpublished data) indicate that neither food availability nor Ca availability fully explain observed differences in the life histories of these two populations. Starch gel electrophoresis (Cox and Hornbach, 1983 and unpublished data) does indicate there are genetic differences between these populations. It appears, then, that clams from RP are adapted for the very harsh conditions of this pond and have decreased overall metabolism including growth and reproduction in response to environmental stress.

While this study does not consider all aspects of the population energetics of *Pisidium casertanum,* it does illus-

Table 5. Values of $\mathring{V}_{O_2}$ at various temperatures for 3 sizes (0.01, 0.10 and 1.00 mg AFDW) of *Pisidium casertanum* from 4 populations: Riopel Pond RP-this study), Farriers Pond (FP-this study), Lake Pääjärvi (PA-Holopainen and Ranta, 1977b) and Lake Esrom (ES-Berg and Jonasson, 1965).

Temperature (°C)	$\mathring{V}_{O_2}$ from 4 populations for 0.01 mg clams				Ratios of $\mathring{V}_{O_2}$ relative to RP population		
	RP	FP	PA	ES	FP/RP	PA/RP	ES/RP
5	0.005	0.006	0.002	—	1.2	0.4	—
10	0.001	0.003	0.003	—	3.0	3.0	—
20	0.033	0.003	0.011	—	11.0	3.7	—
25	0.004	0.010	—	—	2.5	—	—
30	0.016	0.024	—	—	1.5	—	—
	$\mathring{V}_{O_2}$ for 0.10 mg clams				Ratios of $\mathring{V}_{O_2}$ relative to RP populations		
5	0.027	0.030	0.011	—	1.1	0.4	—
10	0.012	0.037	0.015	—	3.1	1.3	—
20	0.017	0.105	0.074	—	6.2	4.4	—
25	0.020	0.051	—	—	2.6	—	—
30	0.043	0.056	—	—	1.3	—	—
	$\mathring{V}_{O_2}$ for 1.00 mg clams				Ratios of $\mathring{V}_{O_2}$ relative to RP population		
5	0.156	0.144	0.060	0.114*	0.9	0.4	0.7
10	0.149	0.417	0.082	0.191*	2.8	0.6	1.3
20	0.114	0.333	0.485	—	2.9	4.3	—
25	0.102	0.273	—	—	2.7	—	—
30	0.119	0.129	—	—	1.1	—	—

*Extrapolated from values for 2 mg live weight (= approx. 0.72 mg ash free dry weight) assuming b-value of 0.73

Table 6. Habitat and life history parameters for 4 populations of *Pisidium casertanum*.

		Population		
	Riopel Pond	Farriers Pond	Lake Pääjärvi	Lake Esrom
Depth at Which Population Collected (m)	1	1	5	20
Annual Range of Temperature (C)	3–28	3–31	1–23	2–16
Conductivity (μmho·cm^{-1})	10–17	230–280	69	160–320
Minimum Free-Living Shell Length (mm)	0.6	0.7	0.8	0.9
Maximum Shell Length (mm)	3.3	4.8	4.3	4.2
Adult Size at Maturity* (mm)	2.2	2.4	2.2	2.4
Maximum Embryo Length (mm)	0.9	1.0	1.1	1.0
Maximum Number of Embryos/Adult	16	34	27	20
Life Span (yr)	2–3**	2–3**	3	4–5
Reference	Cox and Hornbach, 1983 and unpubl. data.	Cox and Hornbach, 1983 and unpubl. data.	Holopainen, 1978	Jonasson, 1972; Holopainen and Jonasson, 1983.

*containing extramarsupial larvae

**based on continuing laboratory studies (unpublished data)

trate the point that intra-specific variation in metabolic rate can be great. It further illustrates that factors other than size, temperature, and season can influence metabolic rates. It also appears that there is a strong correlation between absolute levels of metabolism and life history traits in pisidiid clams.

SUMMARY

In this paper I have attempted to review the major aspects of metabolism in the pisidiid clams. While data from the literature can be found for 37 populations of these clams, few studies have dealt systematically with the examination of the many factors which can influence metabolic rates. The most obvious results of this review is that there is a great deal of variation in the metabolic rates in pisidiids and this variability seems to allow specific populations to be adapted for local conditions. Even though there is this great variability a few generalizations can be made regarding the patterns of metabolism in this group.

1. Values of the exponent, b, from the weight-metabolic rate equation $\overset{\circ}{V}_{0_2} = aW^b$, vary greatly in this group. There are seasonal variations. However, intraspecifically a b-value near 1.0 is often found during periods of reproduction indicating that the presence of incubating larvae may increase the metabolic rates of gravid adults such that there weight-specific metabolic rates are the same as juveniles.

2. Across genera, b-values are not significantly different for clams whose metabolic rates were determined at 20°C, and averages 0.89. Size then appears to affect metabolism in a consistent fashion across species and genera in this family.

3. Values of Q_{10} range from 0.2–14.8 in this family. Various studies show that Q_{10} varies with season and size. No difference was found between the range of Q_{10}'s reported for summer and winter acclimated animals nor were there significant differences in Q_{10} ranges between genera.

4. As expected from the lack of correlation between season and Q_{10} values, a variety of acclimation patterns have been described in this family. The most common are Precht's Type I (over compensation) and Type V (reverse acclimation). These two patterns have been explained as adaptive for they allow for exploitation of resources and energy conservation (dependent on prevailing environmental conditions) especially during times of reproduction and growth.

5. Pisidiids can survive in anaerobic environments. Metabolic rates (measured as 0_2 consumed) decline at low levels of oxygen. Some species show independence of metabolic rate on 0_2 availability at higher 0_2 levels while others show stricter conformity. Anaerobic metabolism *per se* has not been examined in these forms, however, they do appear to have the enzymes necessary for alternative anerobic metabolic pathways.

6. The efficiency of production (production:assimilation) varies from 10 to 79% in this group. There are no significant differences in this efficiency among genera. The genus *Pisidium* does, however, have a lower weight-specific metabolic rate than either *Musculium* or *Sphaerium.* This lowered rate of metabolism linked with a similar production efficiency suggests that members of the genus *Pisidium* should have a lower weight specific production. Values of production:biomass are indeed lowest in *Pisidium*. The lower weight-specific production may be responsible for the lowered reproductive capabilities of *Pisidium*.

7. An example of intraspecific variation in *Pisidium casertanum* demonstrates that environment can greatly influence metabolic rates. Clams from a pond deficient in ions have lowered metabolic rates than clams from other, more ion rich environments. These differences in overall metabolism are reflected in differential life-histories. Clams from the ion-poor environment are smaller in size and produce fewer young than the clams from the other populations.

8. There is a need for greater examination of metabolism in relation to specific life histories of freshwater clams in order to assess the strategies involved in the optimal partitioning of energy to various life-processes.

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SEASONAL RESPONSES OF FILTRATION RATES TO TEMPERATURE, OXYGEN AVAILABILITY, AND PARTICLE CONCENTRATION OF THE FRESHWATER CLAM *MUSCULIUM PARTUMEIUM* (SAY)

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ABSTRACT

Seasonal filtration rates of a pond population of the freshwater pisidiid clam, *Musculium partumeium* (Say), were assessed by measuring the clearance of 2.02 μm latex beads from suspension and expressed in terms of $FR = a(AFDW)^b$ where FR = filtration rate (ml $H_20 \cdot hr^{-1}$), AFDW = mg ash-free dry weight of a whole clam and 'a' and 'b' are constants. The a-values (= FR of a 1-mg AFDW clam) vary seasonally with the highest rates corresponding to periods of maximum growth and reproduction in the spring and fall. Changes in 'b' reflect the influence of body size on the weight-specific rates (FR/AFDW). Seasonally 'a' and 'b' are inversely related. Therefore, seasonal increases in FR are proportionately greater for smaller clams. The Q_{10} of FR is between 2–3 during the winter and decreases to 1.0 during the summer (temperature insensitivity) when clams are relatively inactive. At 20°C under aerobic conditions FR decreases as the concentration of suspension increases over a range of $\simeq$ 1.38–40 mg. $\cdot l^{-1}$ with the FR for 1-mg AFDW clams going from 4.8 to 0.5; this minimum FR is maintained at higher concentrations. The amount of filtrate cleared ($\mu g \cdot clam^{-1} \cdot hr^{-1}$) initially increases as concentration increases (to $\simeq$ 13 $mg^{-1} \cdot l$) then decreases before increasing again at concentrations$> \simeq 30$ mg $\cdot l^{-1}$. Ingestion must be less at higher concentrations since pseudofeces are produced at concentrations $>$ 22 mg $\cdot l^{-1}$. Under anaerobic conditions FR is uniformly low at all concentrations.

Seasonal responses of FR are assessed in terms of temperature, oxygen availability and particle concentration, and interpreted in terms of the interaction of growth, reproduction and population dynamics. These data have been integrated for 1-m^2 of pond substrate. It is estimated that the clam population ingests 13.81 gC $\cdot m^{-2} \cdot yr^{-1}$. It is suggested that *M. partumeium* probably supplements filter-feeding with other mechanisms of energy intake such as deposit-feeding.

In freshwater ecosystems the two major groups of benthic filter feeders are the insect larvae and bivalves: until recently most attention has been focused on the role of insects (e.g., McCullough et al., 1979; Wallace and Merritt, 1980). However the importance of the role of filter feeding in freshwater bivalves has received attention (e.g., Stańczykowska et al., 1976; Walz, 1978; Cohen et al., 1984); and recently Burky (1983) reviewed some of the studies on the physiological ecology of freshwater bivalves. Through filter-feeding particulate material is either ingested or consolidated as pseudofeces. This makes energy available to the clams as well as to other trophic levels (Kuenzler, 1961a,b).

The Unionacea and Corbiculacea constitute the two major superfamilies of freshwater bivalves. The pisidiids (family Pisidiidae, superfamily Corbiculacea) are a hermaphroditic and viviparous group which includes *Musculium partumeium.* The tiny pisidiids are widely distributed and often dominate the benthos in biomass and/or numbers (references in Burky, 1983). They also serve as food for predators such as insects (Foote, 1976), fish (Eyerdam, 1968; Jude, 1973; Frank, 1980) and waterfowl (Thompson, 1973). Reports on the filter-feeding of freshwater molluscs have involved gastropods (e.g., Mattice, 1972; Tashiro and Coleman, 1982; references in Aldridge, 1983) and clams (references in Burky, 1983; and McMahon, 1983). Studies on the

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filtration dynamics of pisidiids have been reported (Alimov, 1965; Mitropolskii, 1966; Alimov and Bulion, 1972; Benedens and Hinz, 1980; Hornbach et al., 1984). Seasonal adaptations of filtration rates have further effects on clams and the ecosystem (Burky, 1983). However, only the studies of Hornbach et al. (1984) on *Sphaerium striatinum* and this study on *M. partumeium* examine the influence of season on feeding.

This report presents seasonal changes in filtration rate for a permanent pond population of the freshwater clam, *Musculium partumeium.* The effects of particle concentration, oxygen availability, temperature, and body size on filter-feeding are interpreted in terms of the interaction of growth, reproduction, and population dynamics.

MATERIALS AND METHODS

Clams are located in the permanent marsh pond at the Aullwood Audubon Center and Farm which is operated by the National Audubon Society (USGS map quadrangle, Trotwood, Ohio: 39°52.22′N; 84°15.80′W; specimens are on deposit with the Museum of Zoology, University of Michigan, Ann Arbor, USA, voucher No. 250037). In other publications (Hornbach et al., 1980; Way et al., 1980; Burky et al., 1985) AM is used to refer to this permanent pond population. The pond has a surface area of 396 m^2 and a maximum depth of 0.7 m. This pond experiences low oxygen concentrations or is anoxic over most of the period from mid-May through late September. A more detailed description of the pond can be found in Way et al., (1980). In order to judge this study on the seasonal filtration dynamics of *M. partumeium* it is necessary to outline some basic aspects of life-history for the population from Way et al. (1980), Hornbach et al. (1980), and Burky et al. 1985. The population has two generations per year. Recruitment of the spring generation occurs in May–July, growth begins in August–September after a dormant period and they give birth in September–November. Some spring generation adults overwinter and contribute to reproduction in the spring. Recruitment of the fall generation occurs in September-November. The fall recruits overwinter as "subadults" with rapid growth and reproduction in the spring. Most clams of the fall generation die by the end of July with a few surviving to make a small contribution to fall reproduction.

Clams were taken from the pond substrate and vegetation by washing with 0.5-mm sieves (usually before 0800 hr), placed in Thermos bottles and returned to the laboratory where filtration experiments were run the same day under conditions of constant light and oxygen saturation. The conditions of collection, transportation and holding provide oxygen saturation for a few hours before experimental runs. Filtration rates were measured using the method of Burky and Benjamin (1979). Seasonal filtration rates were determined at field temperature and other experimental temperatures using a suspension of 2.02 μm diameter (S.D. = 0.135 μm) PVT (polyvinyltoluene) beads in prefiltered pond water at a concentration of 22 mg · l^{-1}. Clams were rinsed with filtered pond water prior to sorting into 7–16 categories (usually > 9) of one to fifty depending on size (1.5 mm to ≃ 8.0 mm shell length). Each group was placed in a 50 ml Erlenmeyer flask with 10 ml of filtered pond water and allowed to equilibrate for 30 minutes. Ten ml of concentrated PVT suspension was added to each chamber (to bring it to 22 mg PVT · l^{-1}) and initially stirred. After 1–4 hr (depending on temperature and season) a 10 ml aliquot was taken from each flask (mucus, feces, and pseudofeces were avoided) and dried at 95°C for 24 hr. The dry PVT beads were dissolved in 2.0 ml of dioxane and absorbances read at 267 mμ on a Beckman DU spectrophotometer using dioxane as the optical blank. The initial PVT concentration without clams (control flask) and filtered pond water without clams or PVT beads (water-blank flasks) were treated the same as experimental flasks. The final concentration of PVT in both experimental and control flasks is proportional to the observed optical density minus the optical density of the water-blank. Filtration rates were calculated using a modification of the clearance equation of Coughlan (1969):

$$FR = \frac{V}{n} \cdot \frac{\log_{10}(A_c - A_b) - \log_{10}(A_s - A_b)}{\log_{10} e \cdot t}$$

where FR = filtration rate or water clearance rate (ml $H_2O \cdot \mathrm{clam}^{-1} \cdot \mathrm{hr}^{-1}$);
V = volume of experimental PVT suspension (ml);
n = number of clams used;
A_c = absorbance reading for control;
A_b = absorbance reading for water blank;
A_s = absorbance reading for experimental sample;
A_e = 2.71828 . . .; and
A_t = time of run (hr).

Upon the completion of each experiment, clams were fixed in 12% neutral formalin, maximum shell length (anterior-posterior dimension) measured to the nearest 0.1 mm with a stage micrometer on a dissecting microscope, and dried to constant weight at 95°C.

For *M. partumeium* from AM the percentage of dry tissue weight (excluding shell) present in all size categories is essentially 18.2% of total dry weight (shell + tissue) (Burky et al., 1979). All measurements of total dry weight (shell + tissue) have been converted to dry tissue (or AFDW = ash-free dry weight) using this relationship.

Filtration rates were determined under aerobic conditions of oxygen saturation at 20°C for seven concentrations of PVT (1.38–88 mg · l^{-1}); rates for sucessive concentrations were determined on 6–9 size categories of clams over a period of seven days in July. Filtration rates were also determined under "anaerobic" conditions (0–2.5 mg0$_2$ · l^{-1}) at 20°C for five concentrations of PVT (2.75–44 mg · l^{-1}); rates for successive concentrations were determined on 6–8 size categories of clams over a period of five days in July–August. Low oxygen concentrations were achieved by bubbling nitrogen through the water and PVT suspensions, and rubber stoppers were subsequently placed on each flask. Oxygen concentration was checked by the Winkler method at the end of experimental runs.

For each set of experimental conditions there were usually > 9 size groups of clams yielding data pairs of average body size (mg AFDW) and filtration rate (ml $H_20 \cdot clam^{-1} \cdot hr^{-1}$). The regression of $\log_e$ FR and $\log_e$ size (e.g. AFDW) form a linear relationship using the power curve equation:

$$FR = a(AFDW)^b$$

where AFDW = mg ash-free dry weight of a whole clam;
a = constant, equivalent to the FR of a 1-mg AFDW standard clam; and
b = constant and slope of the linear relationship.

The regression constants ('a' and 'b') form an important basis for making comparisons. Changes in 'a' represent absolute shifts in FR for the given conditions while changes in 'b' represent relative changes in FR according to size: $b > 1$ gives lower weight-specific rates (FR/AFDW) for smaller clams; $b = 1$ gives equal weight-specific rates for clams of all sizes; and $b < 1$ gives higher weight-specific rates for smaller clams. The regression statistics are predicted in log space and are symmetrical in log space. When FR values are converted to arithmetic space the resulting confidence limits about the predicted FRs are asymmetrical. This asymmetry accurately reflects the limits of resolution inherent when rates are measured in a depletion system.

The Q_{10} of filtration was determined from the seasonal experiments at two different temperatures (field and experimental). The ratios of the predicted filtration rates for a 1-mg AFDW standard clam ('a') were used as the representative response of the population and to predict FRs at 10°C.

The concentration of suspended particulate matter in the AM pond was quantified in terms of both total dry weight (total suspended solids: TSS) and oxidizable carbon (suspended organic carbon: SOC). Samples were taken before 0800 hr from undisturbed areas of the middle layer of the water column ($\simeq$ 0.25 m below the surface). A modified aquarium cleaner consisting of a section of plastic tubing and a hand pump was used to take water samples. A coarse nylon mesh (1.0 mm^2) over the inhalent pipe prevented the aspiration of gross debris such as leaves or insects. The sample was poured through 0.2 mm^2 mesh bolting cloth in the laboratory to remove particles including some living organisms. A known volume of the remaining suspension was then aspirated with a Millipore apparatus through a tared glass filter (2.4 cm diameter Whatman GF/B, effective retention > 1.0 μm particles: filters were prepared by heating for 30 minutes at 450–500°C in a muffle furnace, to remove oxidizable contaminants, Strickland and Parsons, 1965). Six samples were taken in this manner on specific dates. Filters (with filtrate) were dried for four hours at 60°C, weighed, sealed with foil, and subsequently stored in a dessicator. Organic carbon content of filtrate was determined using the wet oxidation method of Russell-Hunter et al. (1968).

RESULTS

The seasonal filtration rates are summarized as regression coefficients for $FR = a(AFDW)^b$ in Table 1. This is illustrated for the field temperature data of Table 1 in Figure 1 for predictions based on AFDW. Overwintering clams (fall recruits) of birth size (spat, average shell length $<$ 1.8 mm) have experienced little or no growth by mid-March when rapid growth and FRs are initiated. Spat of the spring recruitment (late May) have comparatively clean shells and can easily be separated from the few overwintering spat that remain at this time. The overwintering spat have high FRs while the spring recruits are dormant after birth (May–August); they (spring recruits) behave differently (dormant, low FRs) from the rest of the population during the summer in this permanent pond. The FRs of this uniform size group of spring-born spat are therefore treated separately as means rather than as predictions from the power curve equation. Predictions of FR for clams with an AFDW of 0.2 mg are given in Figure 1. Clams with mean AFDWs of 0.05, 0.2 and 1.0 mg are equivalent to clams with shell lengths of $\simeq$ 1.4, 3.0, and 5.0 mm respectively. A 1-mg AFDW standard clam (5.0 mm shell length) is an adult of modal size.

The a-values (Table 1, Fig. 1) are indicative of filtration rates as both the whole animal rate and as the weight-specific rate for a 1-mg AFDW standard clam (ml $H_20 \cdot clam^{-1} \cdot hr^{-1}$ = ml $H_20 \cdot$ mg $AFDW^{-1} \cdot hr^{-1}$ only for a 1-mg AFDW clam). The a-value increases to a maximum in April–June with the suggestion of a second peak in November. Changes in b-value represent the influence of size on changes in FR. During late fall and winter 'b' is a little greater than 1.0. The b-value decreases from 1.0 (February–March) to 0.46 in April. There is an increase in 'b' through the summer to 1.2 in September with a subsequent decrease during October–November to 0.7. Lower values of 'b' suggest that smaller clams have higher relative weight-specific rates (FR/AFDW). Over most of the year there is an inverse relationship between 'a' and 'b' (i.e., as 'a' increases 'b' decreases) with major decreases of 'b' associated with major periods of growth and reproduction in the spring and late fall. This shows that the absolute increases in filtration are proportionately greater for smaller clams at these times. The high b-value (1.2) in September probably reflects reproductive condition and the carrying of broods by larger clams. Conversely, spring growth and reproduction are only associated with b-values below 1.0. This suggests that the interaction of the energetic demands and the dynamics of filtration are different during the spring and fall. Predictions of weight-specific filtration (FR/AFDW) for smaller clams (0.2 mg AFDW) emphasize the effects of changes in 'b' (Fig. 1).

Early spring brings about a rapid increase in the filtration rates of clams of all sizes; spat and small adults (e.g. 0.2 mg AFDW) display significantly higher weight-specific rates than larger animals (Fig. 1). During the spring, overwintering spat grow into small adults, whose weight-specific filtration rates become indistinguishable from larger adults as 'b'

Table 1. Regression coefficients for FR = $a(AFDW)^b$ at field and experimental temperatures where FR = filtration rate (ml $H_2O \cdot clam^{-1} \cdot hr^{-1}$) and AFDW = mg ash-free dry weight of a whole clam.

Date	Number of determinations	Field temperature °C	Experimental temperature °C	a	b	r^2
7-26-77	7	16	16	0.745	0.863	0.703
7-26-77	7	16	21	0.641	0.552	0.483
9-18-77	16	22	22	0.583	1.180	0.845
10-15-77	10	9	9	0.501	0.797	0.846
10-15-77	10	9	19	0.644	1.090	0.802
11-23-77	10	8	8	0.952	0.693	0.696
11-23-77	9	8	18	1.510	0.615	0.800
12-15-77	12	5	5	0.348	1.190	0.782
12-15-77	12	5	15	0.769	0.703	0.493
3-7-78	9	1	1	0.309	0.984	0.933
3-7-78	9	1	10	0.762	0.513	0.148
3-22-78	11	7	7	1.271	0.786	0.934
3-22-78	11	7	17	1.774	0.819	0.758
4-11-78	14	13	13	2.080	0.462	0.827
4-11-78	13	13	23	2.489	0.399	0.675
5-5-78	13	10	10	2.084	0.569	0.795
5-5-78	13	10	20	1.941	0.561	0.856
5-22-78	13	12	12	1.888	0.736	0.840
5-22-78	13	12	22	1.795	0.731	0.837

approaches 1.0 by late July. All adults show a decrease in absolute filtration activity ('a') during the summer.

Spat born during the spring filter at an extremely low rate throughout the summer (dormancy). Although the spring recruits are known to mature into adults during late summer (Way, et al. 1980), no corresponding increase in filtration rate was observed. The gap in data from mid-August to mid-September probably missed this event, as growth is initiated rapidly. Spat born during the fall filter at low rates; these rates are maintained throughout the winter, until March when growth is resumed. A second peak of spat activity is observed in November and corresponds to a peak in adult activity at that time. However, the November value is based on only one measurement of a group of 10 spat and may be an artifact.

Figure 2 illustrates the response of filtration to temperature (Q_{10}), and gives the predicted rates (a-values) for field-acclimated animals at 10°C and at field temperature. Q_{10} ratios are significantly different from 1.0 only during December. However, the seasonal trends appear real, since there is a steady decrease of Q_{10} until July; Q_{10} values increase through the fall. The response of filtration to temperature is minimal (temperature insensitive) during warmer months (April–October) when Q_{10} is essentially 1.0. Q_{10} values above 1.0 in the winter months indicate that while *M. partumeium* shows a strategy of low activity (low winter a-values), diurnal temperature increases and warming trends (winter thaws or spring) may be exploited.

The amount of available suspended organic carbon (SOC) and total suspended solids (TSS) in the pond water varies significantly over the year (Fig. 3). Seasonal patterns of FR (Figs. 1 and 2) do not follow trends of available SOC, and periods of high SOC do not appear to be exploited (see Discussion). The highest FRs (March–June) occur during a time of modest SOC availability. It should be pointed out that seasonal FRs were determined using suspensions at 22 mg PVT $\cdot$ l^{-1} while the TSS in the pond range from 0.88 to 17 mg $\cdot$ l^{-1}.

The relationship between FR and polyvinyltoluene bead (PVT) concentration are given in Figure 4. For each concentration of PVT the a-values [from FR = $a(AFDW)^b$] are used to make comparisons of rates for a standard size clam. Under conditions of low oxygen availability FRs are very low at all concentrations of PVT. Under conditions of oxygen saturation there is an inverse relationship between FR and PVT concentration with FR reaching a low asymptote at concentrations $>$ 40 mg PVT $\cdot$ l^{-1}. This type of non-linear relationship between FR and mg PVT $\cdot$ l^{-1} can be expressed by the following equation (Poole, 1974):

$$FR = A + [B(R)^{conc}]$$

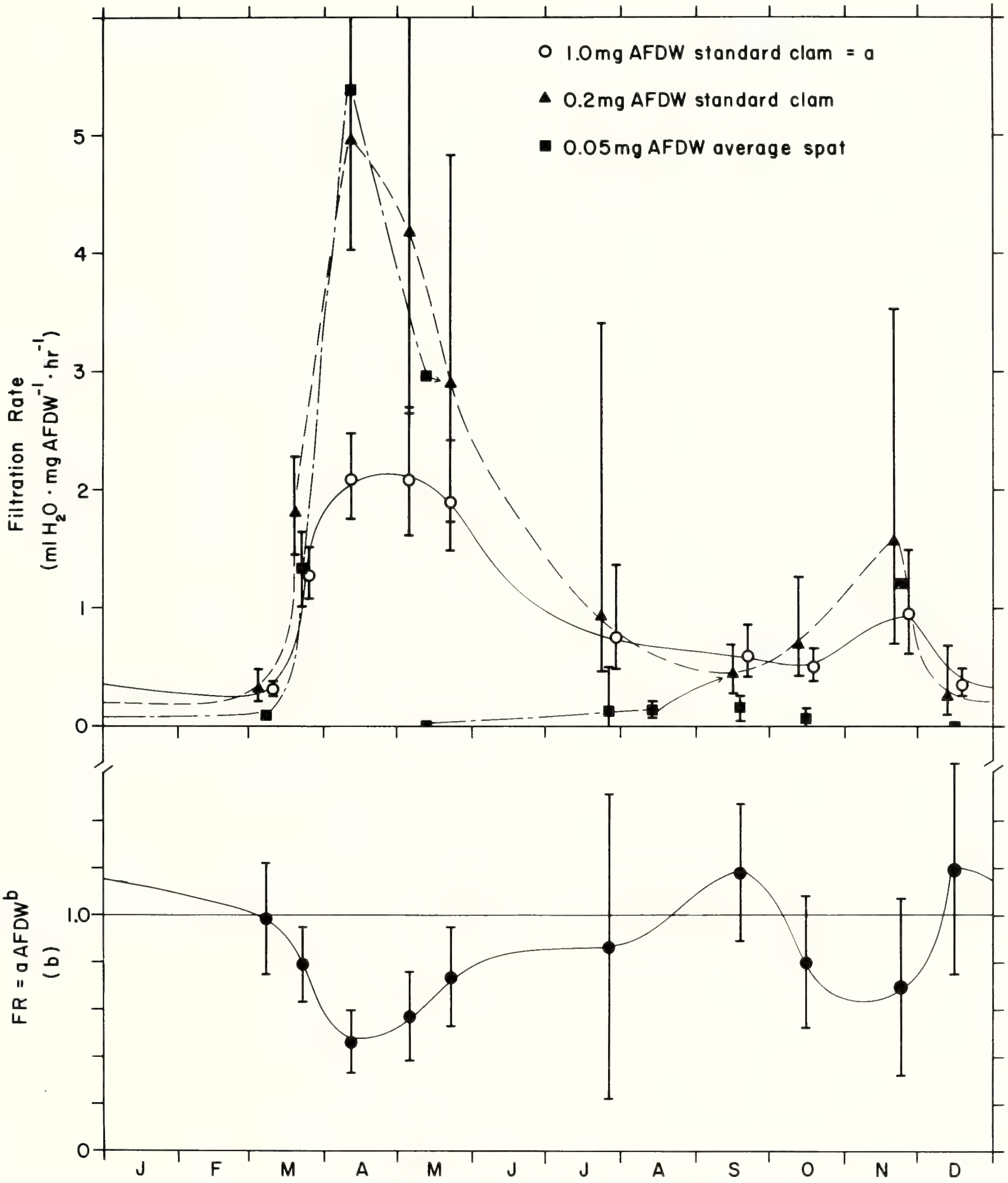

Fig. 1. Seasonal weight-specific filtration rates and regression coefficients ['a' and 'b' from FR = a(AFDW)^b] for *Musculium partumeium* at field temperatures. Vertical bars represent 95% confidence limits. All determinations were made on the dates for the rates of 1-mg AFDW clams. Offset plotting is used to avoid overlap. Arrows from values for spat to values for 0.2 mg AFDW clams in May and August–September indicate the growth of animals to the next standard size category.

where FR = filtration rate or water clearance rate of a 1-mg AFDW clam (a-value);
A = asymptotic or minimum value of FR;
B = difference between A and the value of FR when concentration is zero;
R = ratio of successive differences along the curve; and
conc = PVT concentration ($\mathrm{mg \cdot l^{-1}}$).

The equation is given in Figure 4 and provides a reasonable approximation of the relationship.

The rate of particle retention (PVT cleared) can be predicted for each concentration by multiplying FR (= a-value for a 1-mg AFDW clam) by the concentration ($\mathrm{mg\ PVT \cdot l^{-1}}$) of suspension. This provides retention rates as $\mu\mathrm{g\ PVT \cdot standard\ clam^{-1} \cdot hr^{-1}}$ as given in Figure 5. As concentration increases the rate of PVT retention increases rapidly to a peak ($\simeq$ 14 $\mathrm{mg\ PVT \cdot l^{-1}}$), after which the rate decreases slightly as concentration increases to $\simeq$ 30 $\mathrm{mg\ PVT \cdot l^{-1}}$. At concentrations $\geq$ 30 $\mathrm{mg\ PVT \cdot l^{-1}}$, the rate of PVT retention increases even though clearance rates (Fig. 4) are at an asymptotic low above $\simeq$ 40 $\mathrm{mg\ PVT \cdot l^{-1}}$. Pseudofeces are produced at PVT concentrations above 22 $\mathrm{mg\ PVT \cdot l^{-1}}$; the actual ingestion is the amount of suspension filtered minus the pseudofeces produced. Therefore ingestion rates can potentially level off or decrease at higher concentrations.

DISCUSSION

The only study besides this report on *Musculium partumeium* to provide seasonal data for freshwater clams on filtration dynamics in relation to energy budget, life-cycle and ecology of natural populations is the work of Hornbach et al. (1984) on *Sphaerium striatinum.* In this study the filtration rates of *M. partumeium* are interpreted from seasonal predictions of FR (filtration rate) by examining a- and b-values [from FR = $a(\mathrm{AFDW})^b$]. The FR (a-value) peaks in the spring and fall (Fig. 1), corresponding to periods of peak reproduction, and although the absolute clearance rates are higher for larger clams, the weight-specific rates (FR/AFDW) are lower. Smaller clams feed faster and presumably grow faster (Way et al., 1980) as embryos continue to develop in their brood sacs (Hornbach et al., 1980). There is a similar relationship between peak reproduction and peak a-value in *S. striatinum* (Hornbach et al., 1984). However, the changes in a- and b-values take place over longer periods of time for *S. striatinum* because reproduction is spread over a longer period of time and is less synchronous than in *M. partumeium* (Burky, 1983).

Temperature sensitivity changes seasonally for *M. partumeium,* with Q_{10} values between 2 and 3 in December–March and about 1.0 (i.e., temperature insensitivity) in the summer. Buchwalder (1983) studied the same AM population and showed that the b-value of M (M = oxygen consumption of a whole clam = a AFDW^b) increases as temperature increases during the spring and fall periods of growth and reproduction—thus, providing a greater Q_{10} response in M for larger clams. This implies that as temperature increases larger clams are more efficient (aerobic advantage, 'b' of M increases) in energy metabolism even though smaller clams continue to filter at a higher weight-specific rate (b-value of FR shows little or no change as temperature increases, Table 1). During the summer the Q_{10} of M is relatively constant above 2.0 for all sizes of *M. partumeium* and there is an increase in the response of oxygen dependent M (Buchwalder, 1983). This suggests that while the Q_{10} of FR is 1.0 in the summer (Fig. 2), the higher Q_{10} of M along with shifts in oxygen dependent M may help clams exploit available oxygen during periods of low oxygen availability.

There are reports that water clearance rates vary inversely with the concentration of suspended material (Jørgensen, 1975; Winter, 1978). Also, there is evidence that some bivalves maintain feeding currents which are independent of suspension concentration over a broad range of concentrations (Jørgensen, 1966, 1975; Mattice, 1979; Conover et al., 1981). It would appear that there are a number of potential strategies which could produce distinct patterns of response in regard to particle concentration and the rate of water transport. The AM pond varies seasonally in the amount of natural suspended material (Fig. 3). An inverse relationship between clearance rate (FR) and particle concentration is given for *M. partumeium* under aerobic conditions in Fig. 4. A similar relationship has been reported for other freshwater clams by Mitropolskii (1966), Alimov and Bulion (1972) and Hornbach et al., (1984). The rates reported for *Sphaerium corneum* (Mitropolskii, 1966) and *S. striatinum* (Hornbach et al., 1984) are a little higher but roughly comparable to those reported for *M. partumeium.* For *M. partumeium* the decrease in FR as particle concentration increases reaches a low asymptope at $\simeq$ 40 $\mathrm{mg \cdot l^{-1}}$. Under anaerobic conditions FR is uniformly low at all particle concentrations. The rate of particle retention can be predicted if one multiplies FR by the corresponding particle concentration (Fig. 5). Therefore, the rate of particle removal increases rapidly as concentration increases to $\simeq$ 13 $\mathrm{mg \cdot l^{-1}}$. The rate of particle removal decreases slightly between $\simeq$ 13–30 $\cdot\ \mathrm{l^{-1}}$ and then progressively increases as particle concentration increases above $\simeq$ 30 $\mathrm{mg\ PVT \cdot l^{-1}}$ (Fig. 5). Pseudofeces are produced at suspension concentrations greater than the initial peak removal rate in *M. partumeium* (Fig. 5) and in *S. striatinum* (Hornbach et al., 1984). The actual ingestion is the amount of suspension filtered minus pseudofeces production. Therefore, ingestion rate should level off or decrease at higher concentrations of suspension (Winter, 1978; Hornbach et al., 1984). However, the concentration of suspended solids (TSS range: 0.88–17 $\mathrm{mg \cdot l^{-1}}$) in the AM pond are below the concentration when pseudofeces are produced ($\simeq$ 22 $\mathrm{mg\ PVT \cdot l^{-1}}$); the concentration of TSS is usually below the concentration of peak rate of particle removal ($\simeq$ 13 $\mathrm{mg\ PVT \cdot l^{-1}}$). If FR for *M. partumeium* is non-selective in terms of particle size and type (Gale and Lowe, 1971; Winter,

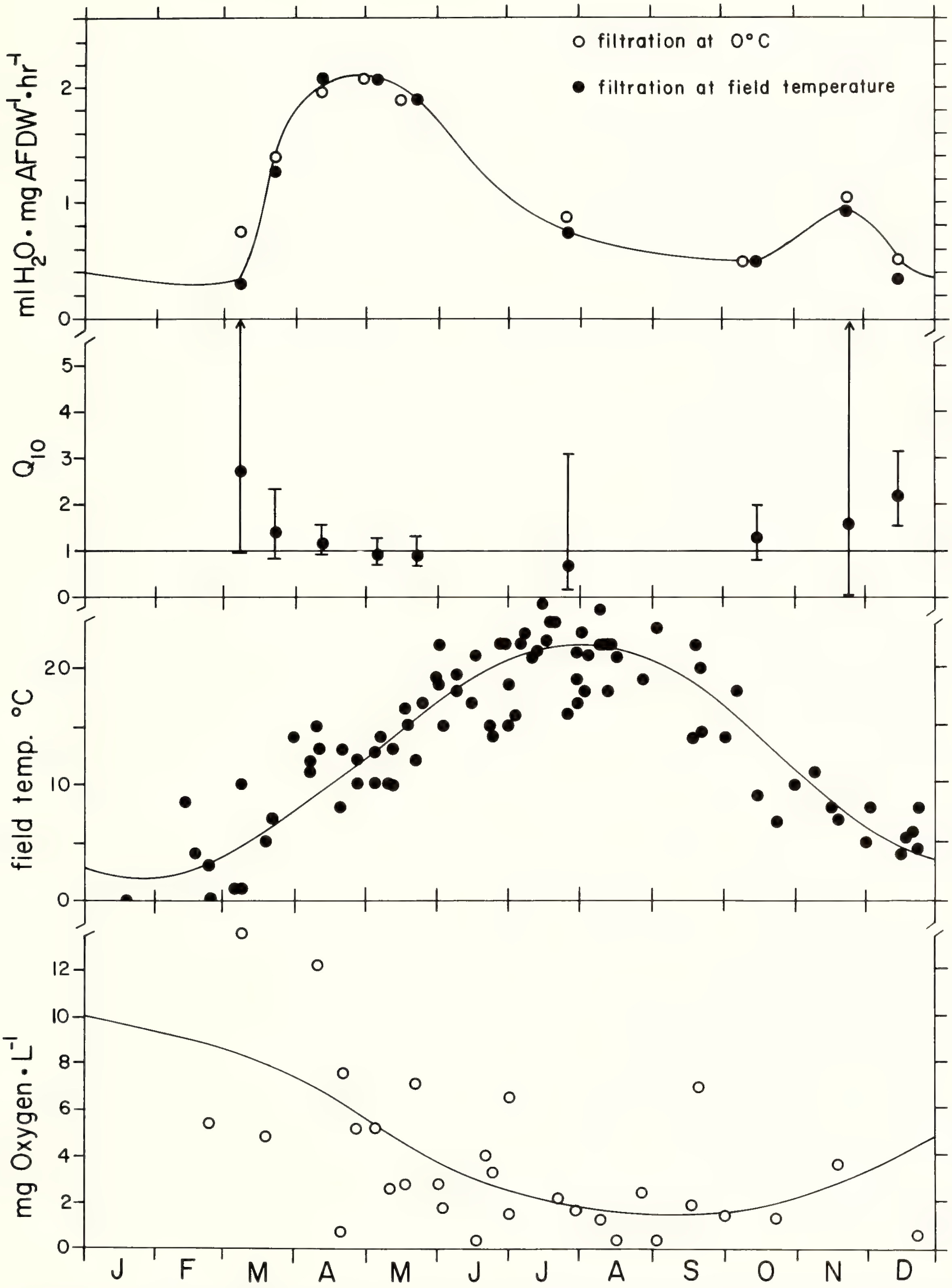

Fig. 2. Filtration rates for 1-mg AFDW standard *Musculium partumeium* at 10°C and field temperature, Q_{10} of filtration with 95% confidence limits, pond temperature and pond oxygen concentratrion in relation to months. Filtration rates were determined on the dates shown for Q_{10}. Offset plotting has been used to avoid the overlap of certain points.

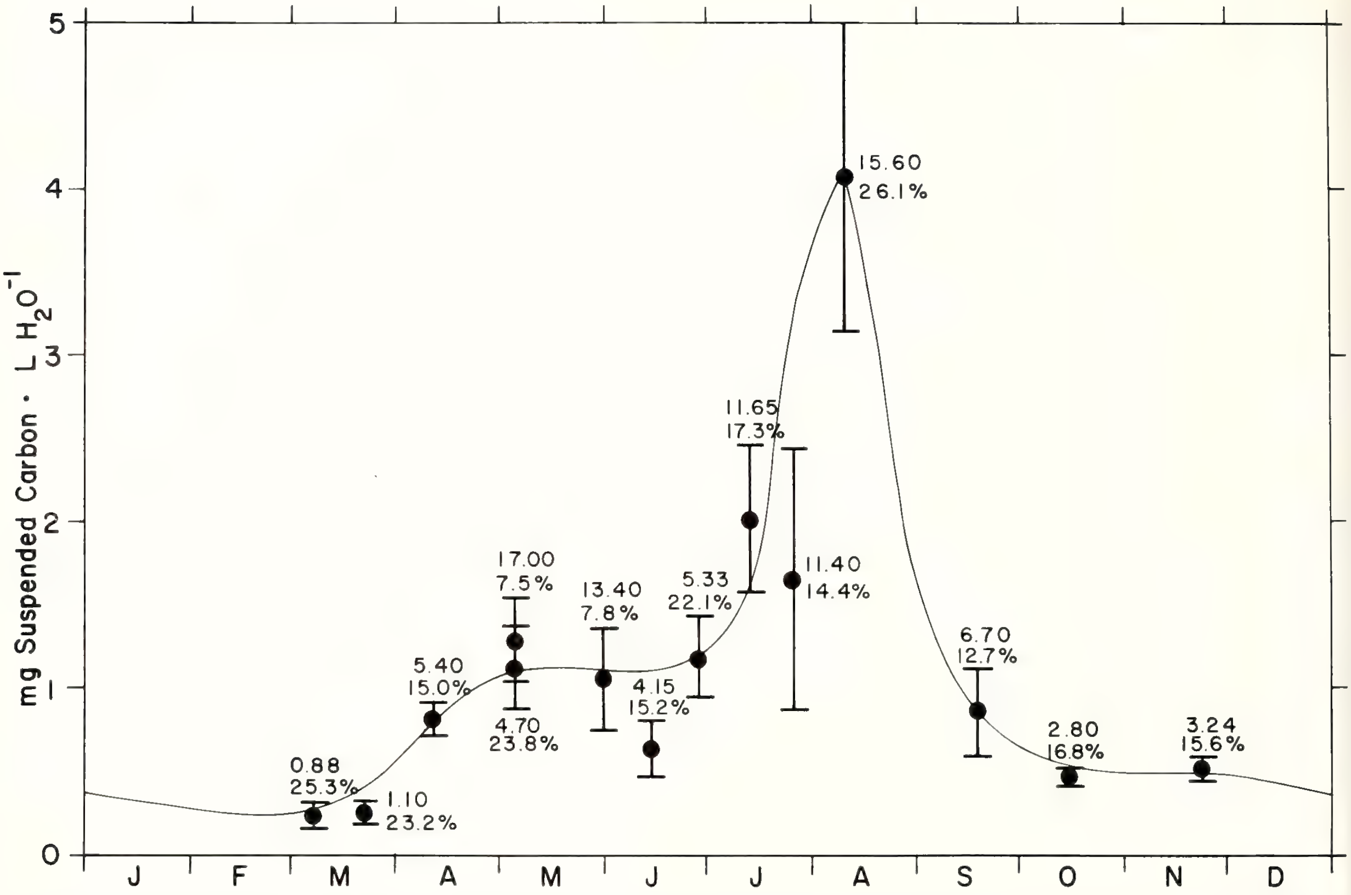

Fig. 3. Suspended organic carbon (SOC) for the Aullwood marsh pond in relation to months. Vertical bars represent the 95% confidence limits. Near each SOC value is the value for total suspended solids (mg TSS · l^{-1}) and the percentage of TSS represented by SOC.

1978), it can be assumed that functional rates of particle removal (based on artificial PVT) of the natural population reflect rates at lower concentrations (Fig. 5) since the concentration of TSS does not exceed 17 mg·l^{-1} in the pond (Fig. 3).

Estimates of population ingestion should also consider diurnal variations in ingestion rate. However, this study measured FR during the morning and all estimates of annual ingestion for *M. partumeium* assume continuous feeding-rates. Although, Winter (1978) and Jørgensen (1975) discuss clams that can be considered to feed continuously, diurnal rhythms have been documented for other bivalves (e.g., Winter, 1978; Benedens and Hinz, 1980). Benedens and Hinz (1980) reported that the minimum diurnal FR for *S. corneum* occurs during the morning (after 0900 hr); this is the time when FRs on *M. partumeium* were measured.

The annual ingestion for the population of *M. partumeium* in the AM pond is estimated as 13.81 gC·m^{-2}·yr^{-1}. This estimate is based on size distributions and density data from the study of Way et al. (1980) for the AM population. These data on population dynamics were integrated with the data of Table 1. These estimates of FR under conditions of oxygen saturation at 22 mg PVT·l^{-1} (l·m^{-2}·day^{-1}) were corrected for the FR response to concentration (Fig. 4) at the appropriate seasonal concentration in the pond (mg TSS·l^{-1}, Fig. 3); values (l·m^{-2}·day^{-1}) were multiplied by the appropriate mg SOC·l^{-1} (Fig. 3) to provide seasonal ingestion rates (mgC·m^{-2}·day^{-1}). The ingestion rates for May–October were further corrected for the effects of low oxygen concentration on FR (Fig. 2 for oxygen level, Fig. 4 for FR response). The rates were weighted according to season and summed to provide the annual ingestion estimate of 13.81 gC·m^{-2}·yr^{-1}. The estimated ingestion value is equal to the annual assimilation estimate of 13.79 gC·m^{-2}·yr^{-1} for the same AM population reported by Burky et al. (1985). This would necessitate an unrealistic assimilation efficiency of 100%. The apparent underestimation of annual ingestion for *M. partumeium* may involve: 1) artificial (e.g., PVT) or inorganic particles may be "unpalatable" and/or not as efficiently filtered as natural

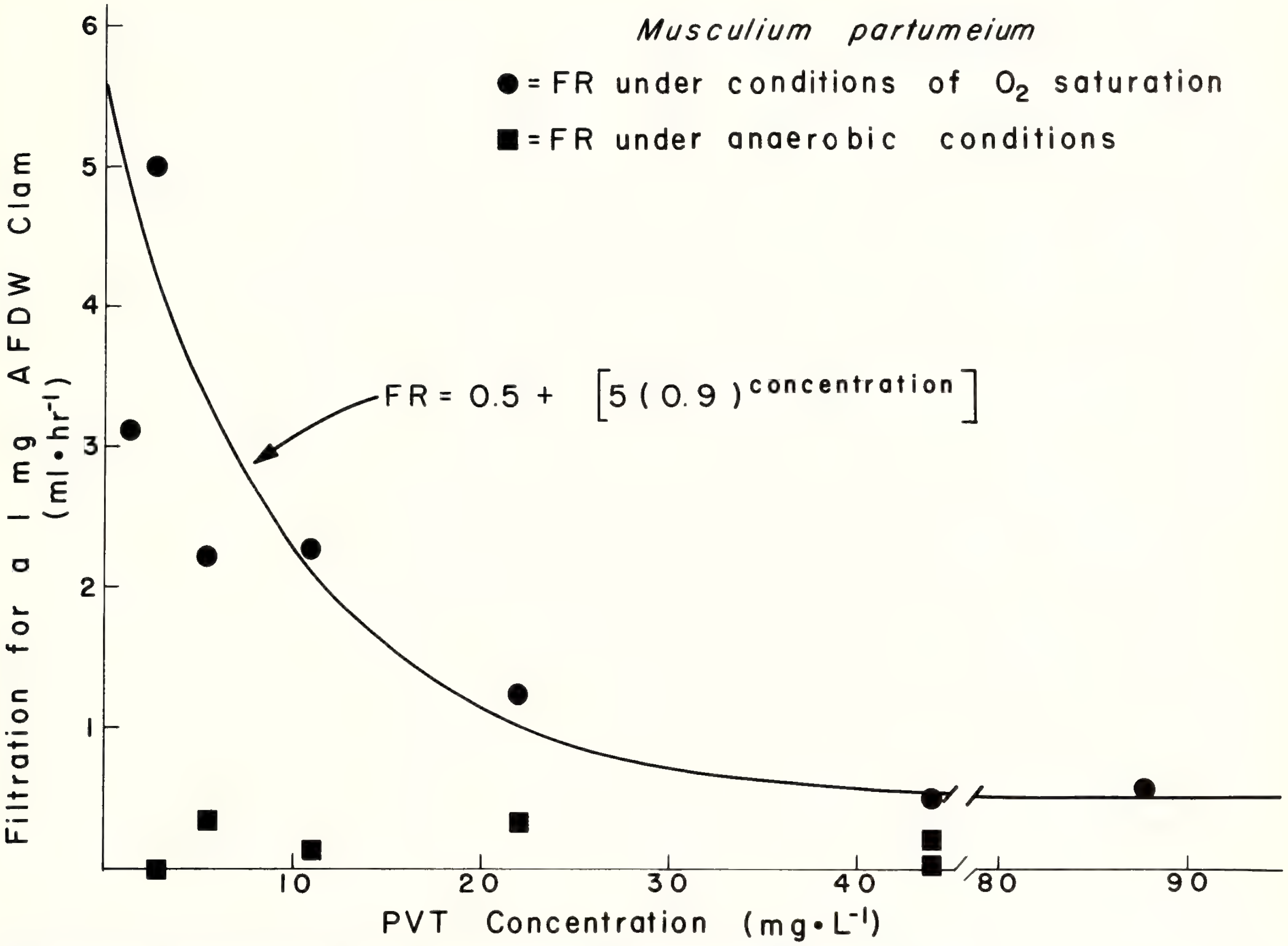

Fig. 4. Relationship between filtration rate for summer-adapted 1-mg AFDW standard *Musculium partumeium* and PVT concentration under aerobic and anerobic conditions at 20°C. The fitted, non-linear equation is given for the relationship under aerobic conditions.

foods (Jørgensen, 1975), however, the rates for *M. partumeium* and *S. striatinum* (rates measured with PVT, Hornbach *et al.,* 1984) compare favorably to those reported for *S. corneum* (rates measured using algae, Mitropolskii, 1966); 2) PVT beads (2.02 μm) may be below the size for efficient particle clearance, however, particles of 1.0 μm can be efficiently retained by some species (e.g., Mohlenberg and Riisgard, 1978; Winter, 1978); 3) morning may represent a time of diurnally low FR; 4) oxygen availability varies diurnally and the effects of generally low levels on FR during the warm months may have been over estimated; and 5) another method of feeding may supplement filter-feeding.

The discrepancies between ingestion and assimilation for *M. partumeium* suggest that some other feeding mechanism may be involved. Effort and Tsumura (1973) demonstrated the direct uptake of dissolved organic material by the pisidiid, *Pisidium casertanum,* but this could only account for less than 4% of the energy budget. *M. partumeium* lives in rich organic substrates of low oxygen concentration and can probably also absorb some dissolved organic compounds. It has also been suggested that deposit feeding is important for a number of pisidiid clams (Mitropoloskii, 1966; Benjamin, 1978; Benjamin and Burky, 1978; Burky, 1983; Hornbach et al., 1984). Species of Pisidium apparently pump water into the mantle cavity along the foot, as well as through normal inhalent areas (Mitropolskii, 1966; Meier-Brook, 1969). This suggests that detritus can be acquired with the use of cilia along the foot as well as through the inhalant siphon. Since *M. partumeium* lives in rich organic (silt) substrates, it is also easy to predict the enrichment (SOC) of the micro-layer of water above the substrate. It is apparent that both filter-feeding and deposit-feeding by tiny clams can be ecologically important if high population density of some populations is considered (e.g., Hinz and Scheil, 1972; Gale, 1975; Way et al., 1980; references in Burky, 1983).

It has been suggested that the life-cycle pattern of *M.*

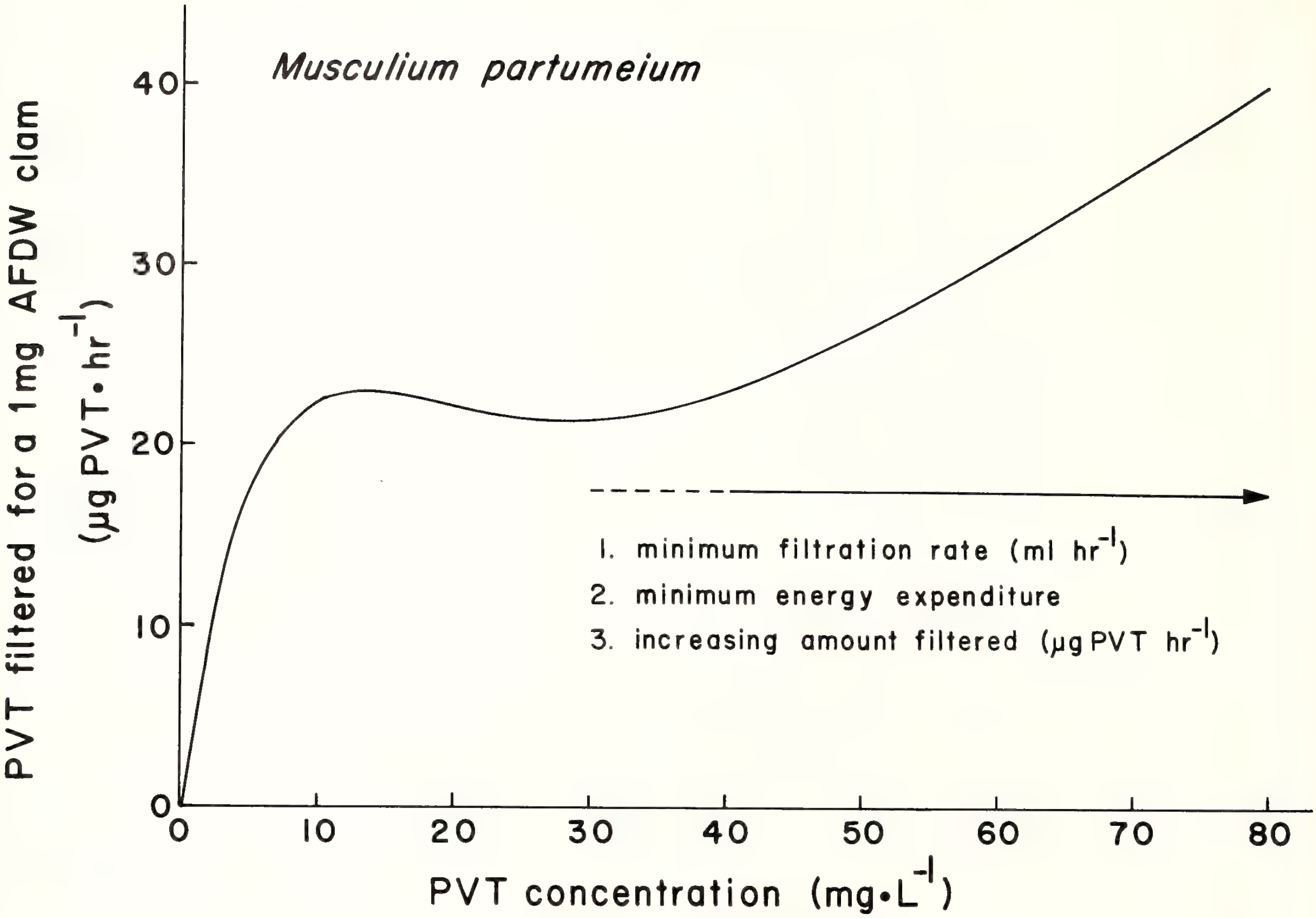

Fig. 5. Relationship between PVT retention rate for summer-adapted 1-mg AFDW standard *Musculium partumieum* and PVT concentration at 20°C. The retention rates (μg PVT · hr^{-1}) are the product of 'a' [from FR = a(AFDW)^b] and the corresponding PVT concentration. The arrow line indicates that (1) minimum filtration rate, (2) minimum energy expenditure, and (3) increasing amount filtered are all achieved at increasing PVT concentrations > 40 mg·l^{-1}.

partumeium evolved in conjunction with predictable events associated with life in temporary pond habitats (potential drying during June–December) and that there is carryover of this life-cycle pattern for populations living in permanent ponds (references given below). This has been extensively documented for the permanent pond population (of this report) and for another population living in a temporary pond (Burky and Benjamin, 1979; Burky et al., 1979; Hornbach et al., 1980; Way et al., 1980, 1981; Conover and Burky, 1981; Conover et al., 1981; McLeod et al., 1981; Buchwalder, 1983; Burky et al., 1985). Further, photoperiod has been suggested as the cue for the control of life-cycle events (Conover and Burky, 1981; discussions in Burky, 1983). The lack of exact correspondence among peak reproduction (and corresponding changes in a- and b-values for FR and M), seasonal changes in Q_{10} of FR and M, seasonal changes in pond temperature, seasonal changes in oxygen availability, and seasonal changes in the concentration of suspended particles suggests that other factors (such as photoperiod) as well as a complex integration of all reported adaptations are involved in the control of clearance rates in *Musculium partumeium*.

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PHYSIOLOGICAL, ECOLOGICAL AND EVOLUTIONARY ASPECTS OF MOLLUSCAN TISSUE DEGROWTH

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ABSTRACT

Natural populations of aquatic molluscs can exhibit degrowth. By the strictest definitions, tissue degrowth of individuals involves a decrease in biomass (including mass of structural proteins). Evidence, from laboratory cultures and natural populations of both gastropod and bivalves, shows that degrowth can be associated with seasonal or reproductive stress. Seven data sets are critically reviewed to establish and quantify the occurrence of molluscan tissue degrowth. The general biological consequences (broadly categorized as physiological, ecological, developmental, and evolutionary) are then discussed in turn. Physiologically, it is important to remember that degrowth and growth of individual molluscs do *not* represent subtractions from (or additions to) some static biomass value, but rather the component rates of biomass turnover falling below or exceeding some equilibrium rate level. Thus studies on the temporal sequence of shifts in catabolic allocation during periods of degrowth are significant. Much recent ecological theory on the evolution of life-cycle patterns hinges on bioenergetic tradeoffs which determine residual reproductive capacity. In these terms, capacity for limited degrowth, which allows decrease in individual energy content to increase survivorship under certain environmental conditions, is paradoxical and compels reconsideration of some fitness predictions involving differential reproductive effort. Capacity for controlled degrowth in flatworms and molluscs may involve dedifferentiation, and potentially even rejuvenation. Phyletically, the indeterminate growth patterns in molluscs contrast with the hormonal close-coupling of sexual maturation with growth pattern in arthropods and in higher vertebrates. Moreover, the molecular bases controlling metameric development in annelid-arthropod stocks may prove to be incompatible with the capacity for degrowth exhibited by flatworms and molluscs, once again illustrating the phylogenetic naiveté of the so-called subkingdom Protostomia or Spiralia.

Capacity for tissue degrowth in molluscs involves complex shifts in metabolism, has ecological consequences at the population level and hence may have considerable evolutionary implications. Before dealing with these physiological, ecological and evolutionary aspects, this paper will attempt a critical survey of certain data sets which provide evidence of molluscan tissue degrowth. The subject is entirely appropriate to a symposium on physiological ecology of freshwater molluscs, since many of the best data are drawn from freshwater pulmonate snails. For convenience, these and other data are considered in seven short sections, three of which draw upon three recent publications from Syracuse, which together form a revealing codicil to the main research efforts there in actuarial bioenergetics of aquatic mollusc populations (Russell-Hunter and Buckley, 1983; and references therein). The data sets can also be claimed as appropriate for an *international* symposium since, although partial and limited, they are biased toward both Scots-American and Dutch sources.

First, there is a need to define degrowth. The best definitions are essentially the opposite of definitions of growth. One good one proposed by Russell-Hunter and Eversole (1976) is that degrowth of an individual animal is a *decrease* in unit mass of structural proteins through time. It is reasonably well established that growth in organisms and in populations should be measured as an increase in organic mass, more specifically as an increase in *ash-free* dry weight (often referred to as tissue dry mass) through time, thus eliminating any biases from changing water content and from skeletal and other structures made up of inorganic salts. Such an increase in the tissue dry mass of an organism could involve carbohydrates, fats or proteins or any combination of the three. In certain long-term studies, it may be appropriate to adopt an even narrower definition limited to increase in structural proteins through time, since carbohydrate reserves may vary from day to day and lipid reserves from season to season. In some animals, energy flux regulation of carbohydrate input and output by a glucostatic mechanism is involved in reducing the extent of such short-term variation. Broadly, therefore, degrowth is decrease in tissue dry mass through time, and narrowly, degrowth is decrease in structural proteins.

When natural populations of aquatic invertebrates continue to exist through periods of starvation, those individual animals that survive have undergone metabolic shifts which affect their whole bioenergetic budgets. More obviously, they may have demonstrated considerable modification of behavior patterns, not only those related to nutrition. Tissue degrowth has been demonstrated to occur in certain flatworms and molluscs [see Calow (1977a, b) and Russell-Hunter and Eversole (1976) for further reference]. Degrowth probably also occurs in several other aquatic invertebrates and some poikilothermic vertebrates.

This paper will use the seven short sections (see Table 1) of critical data review to establish the fact, and quantify the occurrence, of molluscan tissue degrowth, before considering in turn the implications of this capacity for: catabolic physiology, theoretical ecology based on fitness

Table 1. Selected types of data on molluscan tissue degrowth.

Text survey section	mollusc species	type of experiment	source of molluscs	Significant findings on tissue degrowth	Key reference*
1	*Planorbarius corneus*	casual observation	laboratory culture	tissue biomass loss 44% over 126 days with 33% mortality	—
2	*Helisoma trivolvis*	controlled experiment	laboratory culture	tissue biomass loss 50% (protein loss ~20%) over 132 days with 10% mortality; survivors "leaner" (C:N shift 5.78:1 to 4.44:1)	Russell-Hunter and Eversole, 1976
3	*Biomphalaria glabrata*	culture samples	laboratory culture	differential tissue loss from albumen gland and prostate over 84 days	de Jong-Brink, 1973
4	*Mytilus edulis*	field samples	natural population	low point in stored glycogen content mid-March high point in July–August	de Zwaan and Zandee, 1972
5	*Helisoma trivolvis*	physiological rate measures	laboratory culture	protein-carbon conserved in catabolism over 124 days; more-stressed snails compensate better by 80 days	Russell-Hunter, Aldridge, Tashiro and Payne, 1983
6	*Macoma balthica*	field samples	natural population	growth for 3 months, degrowth for 9 months; annual net gain is 50% of growth, mostly protein	Beukema and de Bruin, 1977
7A	*Lymnaea palustris*	natural experiment	8 natural populations	degrowth in ¼ populations, average loss 14.7%, involving 86.4% of individuals	Russell-Hunter, Browne and Aldridge, 1984
7B	*Helisoma trivolvis*			degrowth in ¾ populations, average losses 24.7%, 28.3%, and 41.3%, involving 96.4% of individuals	

*Reference notes: the casual observations of section 1 are from Russell-Hunter (1960, unpublished) summarized in Russell-Hunter and Eversole (1976); additional references to component studies in bivalves are given in the text near the beginning of section 4 and near the end of section 6; additional references on (circumstantial) field evidence of degrowth in freshwater snails are given in the text near the beginning of section 7.

modelling, indeterminate growth patterns and senescence, and the phyletic relationships reflected by patterns of control of development.

DATA SURVEY

The best evidence of degrowth in snails and other shelled molluscs derives from the fact that the shell may carry a record of what a previous tissue biomass for that individual had been. There is an important caveat. It is that ratio measurements, and hence predicted values for tissue, should be obtained only from those species that demonstrably show *no* shell resorption. This caveat rules out the use of component data from a number of species in quantifying degrowth in populations, although observations and calculations based on individuals of these species in the laboratory may still be possible. None of the species with data in Table 1 or reviewed below shows any evidence of shell resorption.

1. Certain early (1959–60) observations concern *Planorbarius corneus,* in which overwinter starvation resulted in shrunken snails "rattling about" inside shells too large for them (Russell-Hunter, 1960 unpublished, summarized in Russell-Hunter and Eversole, 1976). The healthy, active survivors (8/12) showed an average 44% tissue loss over 126 days, calculated on a basis of predicted tissue weights from shell diameters, using a regression (logarithmic transformation) of tissue weight to shell derived from a contemporary field sample (N = 23). Many other people maintaining snails in aquaria must have made similar observations which have gone unquantified or unreported. However for smaller young animals of the same species, Emerson (1967) has reported similar lossess (62.3% with 56% mortality) determined by a different method on snails held at 23° C over 58 days.
2. Evidence for tissue degrowth in *Helisoma trivolvis* from analysis of total organic carbon, combined nitrogen, and tissue dry weight was presented by Russell-Hunter and Eversole (1976). Held in the laboratory in a metabolic framework close to that of natural overwintering, a representative cohort of *Helisoma* showed a 50% loss of tissue biomass (involving perhaps 20% loss of protein) with only 10% mortality over 132 days. The parallel measurements of carbon and nitrogen showed that the snails had significantly lower C:N (carbon: nitrogen) ratios, corresponding to "leaner" snails of proportionately higher protein content despite their smaller tissue size. Computed for modal individuals of fixed shell weight, C:N ratios shifted over 132 days from 5.78:1 to 4.44:1. Thus, since these data were based on individual shell weights, they can be used not only to demonstrate true degrowth (loss of protein) but also to show proportional conservation of protein during tissue loss. Evidence of restricted protein depletion can also be derived from data on experimental starvation presented by von Brand et al. (1948, 1957) on freshwater pulmonates and by Stickle (1971) on the prosobranch *Thais.*
3. Our stricter definition of degrowth in individual snails or in cohorts requires a decrease over time in the mass of structural proteins (Russell-Hunter and Eversole, 1976; Russell-Hunter and Buckley, 1983; and see above) even though, in most cases, tissue degrowth of the individual biomass involves proportionately greater losses of nonproteinaceous tissue components than of the protein fraction. Potentially, loss of structural proteins could involve reduction in cell numbers or modification of cells which can bring about different degrees of dedifferentiation of tissues or of organs. Differential degrowth involving gonads and secondary sex structures, and thus regression from adult status, has been demonstrated in turbellarian flatworms (Reynoldson, 1960, 1961, 1966; Calow, 1977b). There are no parallel field data for any mollusc, and only a single laboratory investigation (de Jong-Brink, 1973) that provides indisputable evidence of dedifferentiation of tissues in a freshwater snail. From component tissue weights and histology in starved *Biomphalaria glabrata* (= *Australorbis glabratus* in other literature), de Jong-Brink shows that there can be differential decreases in secondary sex structures such as albumen gland and prostate. If such changes occur in this vector of *Schistosoma* in field stocks, the possibilities as regards snail population dynamics and parasite transmission rates are far-reaching, although they remain unexplored in detail. Other implications of dedifferentiation as part of the degrowth process will be discussed below.
4. There have been a number of studies of changes in biomass composition for the tissues of commercially important bivalves (for example, Ansell et al., 1964; Ansell and Lander, 1967; Thompson et al., 1974). Processes of degrowth are implicit in their data though not usually discussed as such. An excellent example of this kind of work is that of De Zwaan and Zandee (1972) on distribution and seasonal changes in glycogen content in *Mytilus edulis.* Since individual glycogen values are related to shell weights, it is possible to state that there is a low point in glycogen content in mid-March and a high point in July–August. Such seasonal variations in tissue components have been surveyed for a variety of marine bivalves, but A. G. Eversole has pointed out (personal communication, 1984) that the majority of such seasonal and life-history surveys do not relate their findings to any form of individual shell weight data. Despite this, seasonal shifts in tissue components in temperate marine bivalves (see references near end of section 6, below), and those revealed by parallel analysis of total organic carbon and of combined nitrogen in freshwater snails (see references near beginning of section 7, below), both reflect major seasonal changes in metabolic activity in natural populations and provide circumstantial evidence of degrowth. In an admittedly oversimplified hypothesis which has proved reasonably resilient as a "straw man," Russell-Hunter (1970, 1978) claimed that changes in C:N (carbon:nitrogen) ratios reflected major metabolic changes corresponding to the cycle of biological seasons. Increasing C:N ratios (corresponding possibly to buildup of glycogen or galactogen storage) characterized a period of "preparation" for overwintering, while decreasing C:N ratios (corresponding to buildup of pro-

tein fraction) characterized the prereproductive period. Of course, such assessments of the "standing crop" in tissue components provide only indirect evidence of differential rates of turnover. More recently, direct assessment of the changing proportions of protein-carbon and nonprotein-carbon being used in catabolism has been attempted. When added to rate measures for intake and assimilation of different nutritional components, the catabolic data permit the preparation of dynamic budgets for a clearer understanding of the physiology of tissue biomass changes such as degrowth and growth. Some valuable exceptions among tissue component studies, which *do* incorporate individual shell mass data, will be discussed below (section 6) along with more convincing evidence of degrowth from the estuarine clam *Macoma balthica*.

5. A more recent set of experiments on *Helisoma trivolvis* (Russell-Hunter et al.1983) attempted to elucidate the course of metabolic shifts during the degrowth process. Nearly concurrent assessments of oxygen uptake and nitrogenous excretion can be used to reveal the changing proportions of protein-carbon and nonprotein-carbon being used in catabolism (Bayne and Widdoes, 1978; Aldridge et al., 1980; Aldridge, 1982; Tashiro, 1982). The experiments on *Helisoma* were somewhat less conclusive than might be wished. "Fed" snails were not at satiation, while "unfed" were not totally starved (with microorganisms available in 4-day-old natural water and on each others' shells for grazing). In this kind of experiment with representative cohort groups (twenty groups of eight snails each), experimental provision of polar trophic conditions is impossible empirically. Thus, apart from the controls, the fed experimentals represent a degree of nutritional stress, the unfeds greater stress. Tissue degrowth provided approximately 26% and 18% of the carbon catabolized by unfed and fed snails respectively. There is a clearly controlled differential catabolism of protein resources during degrowth. Weight-specific rates of oxygen uptake and of nitrogenous excretion for both groups showed decreased burning of protein, but rates for the fed snails have increased back to control levels by day 124, while unfed snails decreased utilization of protein for maintenance to about one-third the level of controls. Unfed snails had oxygen uptake rates 45–55% lower than fed snails and, after 124 days starvation, unfed snails had nitrogenous excretion rates 67% lower than fed. Calculated in absolute rate terms, the contribution of protein-carbon to catabolism remains relatively constant, while the contribution of nonprotein-carbon increases during the time course of the experiments for both groups but to a much greater extent for the fed, or less-stressed snails. Once again, the more stressed snails achieve a more effective metabolic compensation during the first eighty days of the experiment. It is clear that more complete actuarial bioenergetics (Russell-Hunter and Buckley, 1983) of molluscan populations will require incorporation into their budgets of better physiological rate data of this sort. It is important to measure the rates of, and changes in, *catabolic* partitioning of protein-carbon and nonprotein-carbon which can accompany the processes both of degrowth and of sustained reproductive effort.

6. One of the few convincing demonstrations of degrowth in a marine bivalve comes from the work of Beukema and de Bruin (1977) on a population of *Macoma balthica* in the Dutch Wadden Sea. From their careful seasonal analyses of ash-free dry tissue weights, lipid contents, glycogen, and total protein, it is possible to deduce an annual cycle of metabolism involving a pronounced and lengthy period of degrowth. In fact, the growing season of adult *Macoma* was limited to the months of April, May and June during which there was a rapid buildup in all tissue components. During the subsequent nine months, the clams lost about 50% of their dry tissue weight—60% of lipids, 85% of glycogen, but only 25% of protein. The result was an annual net growth, almost entirely made up of protein, and amounting to less than 50% of the growth achieved during the brief growing season. The value of this study of *Macoma* comes from its being based on a demographically sampled population in which accurate age determinations were possible, and from the tissue components being related to shell mass (as a power of linear shell measurements).

Parenthetically, it is possible to take the component ratios and "condition factors" of many studies on marine bivalves and deduce degrowth from such circumstantial evidence. Early work on commercially important species like oysters (Walne, 1970) has been paralleled by studies of many bivalve species in cold temperate seas which show seasonal patterns with degrowth phases. The oyster species themselves do not provide useful material for our purposes because shell growth rates are enormously variable and partial shell resorption may occur. However, sets of suitable data are provided by the investigations of Ansell (1972) on *Donax*, Trevallion (1971) on *Tellina*, Hancock and Franklin (1972) on *Cardium*, Ansell (1974) on *Chlamys* and Hughes (1970) on *Scrobicularia*, as well as other studies on *Macoma* in the United States by Gilbert (1973) and in Scotland by Chambers and Milne (1975). All of these studies suggest that significant tissue degrowth occurs overwinter and that the peak of spawning effort often coincides with the seasonal peak of tissue growth. Annual cycles involving alternating periods of growth and degrowth can be more complicated as set out in a valuable paper on scallop bioenergetics (Fuji and Hashizume, 1974), in which organ component weights are related to individual shell heights. In this scallop species, *Patinopecten yessoensis*, there are age-related differences in seasonal peaks of growth, and in growth and reproductive efficiences.

7. Other circumstantial evidence of tissue degrowth had accumulated from a series of investigations into the actuarial bioenergetics of natural populations of freshwater snails (Burky, 1971; Mattice, 1972; Russell-Hunter et al., 1972; Hunter, 1975; McMahon, 1975; Browne, 1978; Eversole, 1978; Russell-Hunter, 1978, Aldridge,1982; and Tashiro, 1982). Observed differential mortalities during overwintering in these pulmonate and prosobranch snail species were

commonly less than mortalities just after breeding, and probably were accompanied by biomass degrowth in the survivors of some cohorts. Such presumptive degrowth in field stocks remains difficult to quantify. New direct field evidence for tissue degrowth was sought from natural populations of *Lymnaea palustris* [probably, more correctly, *Lymnaea* (*Stagnicola*) *elodes*] and of *Helisoma trivolvis*.

Fall and spring samples were taken from four populations of each snail at seven localities in upstate New York (Russell-Hunter et al., 1984). The measure used was decrease in tissue biomass relative to unchanging shell biomass through time (not the stricter measure limited to change in structural proteins). In summary, overwinter growth occurred in one population of *Helisoma* and two populations of *Lymnaea*, while degrowth was demonstrated in three populations of *Helisoma* and one of *Lymnaea*. It was possible to make some correlation of the occurrences of growth and degrowth with abiotic factors in the environment and with natural history of each species. From individual measurements of tissue dry mass (TDM) and of shell CaCO3 mass (SM), it was possible to compute changes in shell:tissue ratios in various ways, and the overwinter changes are significant ($P<.001$) for six of the populations. One of the best ways of assessing overwinter degrowth is to use the regression relationships to TDM to SM from fall samples to predict *individual* TDM values for snails in the spring collections from their actual SM values at that time. We can then express each actual TDM divided by predicted TDM as an individual percentage. These percentage divergences from predicted TDM values, in the four stocks of snails which showed degrowth, correspond to average losses of 24.7%, 28.3% and 41.3% for *Helisoma* populations, and 14.7% for the one *Lymnaea* population in that category. Degrowth in that *Lymnaea* population involved nineteen out of twenty-two individuals and in the three *Helisoma* populations numbered 81 out of 84 individuals, 64 of which exceeded the 20% level of degrowth. That investigation (Russell-Hunter et al., 1984) may prove to be one of the earliest reports of direct field evidence for tissue degrowth occurring overwinter in natural populations of freshwater molluscs.

DISCUSSION OF IMPLICATIONS

Taken together, the seven data sets (Table 1) critically reviewed above provide convincing evidence of the capacity for tissue degrowth in freshwater snails and in commercial bivalves, along with some bioenergetic quantification of the extent of such degrowth. General biological consequences of degrowth—broadly categorized as physiological, ecological, developmental, and evolutionary—can now be discussed in turn. The physiological implications concern the dynamic aspects of catabolism during degrowth and growth, while the ecological ones concern theories based on fitness modelling. In developmental biology, capacity for degrowth has connotations linked to indeterminate growth patterns with facultative senescence, and to phyletic relationships implicit in modes of morphogenesis.

Physiologically, it is very important to treat degrowth, growth, reproductive effort, and other such processes in rate terms (Russell-Hunter and Buckley, 1983). While the individual mollusc is alive, biomass is never static. Degrowth and growth of individuals do *not* represent subtractions from or additions to some static biomass value, but rather the component rates of biomass turnover falling below or exceeding some equilibrium rate value. Degrowth represents a negative value for the *net* combination of input and output as rate functions. Unfortunately, we have no means of obtaining energy-flux levels instantaneously and nondestructively. We have to rely on sequential sampling of mass values (for example of total organic carbon) to provide data to be computed as rates of change through time. In assessing budget tradeoffs and making cohort comparisons, it is especially important to treat ongoing processes like degrowth and reproductive effort in rate terms (Pianka, 1976; Calow, 1979; Russell-Hunter and Buckley, 1983). Thus direct measures of catabolic rates (such as oxygen uptake and nitrogenous excretion) are particularly valuable.

The experiments involving nearly concurrent measurment of oxygen uptake and nitrogenous excretion (see references in section 5 above) can reveal the changing proportions of protein-carbon and nonprotein-carbon being used in catabolism. Changes in catabolic partitioning accompany the degrowth process and it was clear that such metabolic adjustments are more efficient in more stressed stocks. The conservation of protein biomass which may be part of controlled differential catabolism during degrowth has to be conceived as an appropriate parsimony in the net flow-through of amino-acids rather than as the defense of a static contained biomass. More complete actuarial bioenergetics (Russell-Hunter and Buckley, 1983) will require incorporation into their budgets of such directly measured rates of differential catabolism derived from age-structured subsamples from natural populations. In the actuarial program, such rates can also be cross-checked with the appropriate sequential biomass values in a bioenergetic audit process.

For theoretical ecology, some reconsideration of simpler fitness models when applied to molluscan population dynamics must result from any demonstrable capacity for degrowth in the molluscan species being modelled. Fitness is usually defined in such models as lifetime reproductive success. Most models have been developed from the inverse relationship postulated by Fisher (1930) between immediate reproductive effort and parental survival to reproduce again, as modified by the demographic consequences of various life-cycle patterns which were first set out by Lamont Cole (1954). Life-cycle patterns in freshwater molluscs show considerable infraspecific interpopulation variation (Russell-Hunter, 1961, 1978; Calow, 1978, 1983). Despite this, Fisher's inverse relationship can be set out in bioenergetic terms (Russell-Hunter and Buckley, 1983), with relative reproductive effort related to life-cycle pattern and parental survival related to energy conservation for somatic purposes (termed reproductive restraint). Such simpler versions of bioenergetic tradeoff undoubtedly occur in stocks of freshwater molluscs (Browne and Russell-Hunter, 1978; Calow, 1978, 1979; Tashiro, 1982; Buckley 1985). Capacity for limited degrowth, which allows a decrease in individual energy content (organic carbon biomass) to increase survivorship under certain environmental circumstances, is paradoxical in the framework of such simpler models predicting the levels for tradeoffs. According to the most recent survey by Stearns (1980), theoretical studies on the evolution of life-cycle patterns are currently in need of more background knowledge of physiology and development for the organisms concerned. Here we have a case where substantive data on degrowth in natural populations of two freshwater molluscs compels reconsideration of certain fitness predictions about tactical energy budgeting (Russell-Hunter et al., 1984).

The capacity for true degrowth in flatworms and molluscs also has developmental implications, in that it may involve dedifferentiation. Given that recognition of regressed former adults should be easier in populations of shelled molluscs, it is somewhat surprising that the most extensive studies of the effects of seasonal degrowth on population dynamics have been reported for turbellarian flatworms (Reynoldson, 1960, 1961, 1966; Taylor and Reynoldson, 1962; see also Calow and Woollhead, 1977). In general, freshwater flatworms show high resistance to starvation, and their natural populations show dampening of numerical fluctuations as a result of the capacity to resorb tissues which can later be regenerated. One most striking and often quoted example of this concerns lake-dwelling populations of the triclad flatworm *Polycelis tenuis* (Reynoldson, 1960, 1966). During the late-spring period of trophic abundance, immature stocks of *Polycelis* can consist of a mixture of true juveniles and regressed former adult flatworms.

In relation to this extensive dedifferentiation of tissues and organs in flatworms it has been suggested (Child, 1911, 1913, 1914; Calow, 1977b) that postponement of individual senescence can result from rejuvenation of the tissues after degrowth. In particular, Calow (1977b) has suggested that rates of cell growth and redifferentiation after a period of regressive degrowth may affect future survivorship. In turbellarian flatworms at least, we may predict some potential for individual immortality resulting from successive periods of controlled starvation. Although the general capacity for degrowth is a common feature of some flatworms and certain molluscs, direct molluscan evidence for sexual dedifferentiation (and hence rejuvenation) is confined to a single investigation (de Jong-Brink, 1973; see section 3 above). However, there is much circumstantial evidence that, in natural populations of many species of freshwater molluscs, there can be little mortality from endogenous senescence occurring to be detected (Russell-Hunter and Eversole, 1976; Russell-Hunter, 1978). In the sense in which endogenous senescence occurs in all higher vertebrates and in many arthropods, there does not appear to be much evidence of any irreversible ageing in natural populations of aquatic gastropods and bivalves.

In general, the indeterminate growth patterns in molluscs (other than some cephalopods) and in turbellarian flatworms contrast with the hormonal close-coupling of sexual maturation with growth pattern found in arthropods and in higher vertebrates. It is worth listing and briefly reviewing five corollary features of indeterminate growth patterns which are applicable to the majority of bivalves and gastropods. These have been set out almost entirely before (Russell-Hunter and Eversole, 1976; Russell-Hunter et al., 1984) but in a more limited context and with a different emphasis, so that formal reiteration here is expedient, in order to discuss the broader evolutionary aspects of capacity for degrowth.

First, as noted above, unlike arthropods and higher vertebrates, there is *no* definite adult size, and the processes of somatic growth are to some extent independent of the processes of maturation. Secondly, any size parameters that can be defined are more likely to be characteristic of each interbreeding population than they can ever be of the species as a whole (Russell-Hunter, 1961, 1978). There may be extensive intraspecific differences in mean size at first reproduction, or in mean size at death, *among* populations with very little variation *within* each population. The differences between populations in such measures can be highly significant (in many sets of cases with no overlap in their distributions). Thirdly, populations may show capacity for tissue degrowth (and perhaps even dedifferentiation) in response to seasonal stressed circumstances. As discussed above, a decrease in mortality overwinter accompanies a decrease in individual somatic energy content. Under certain environmental conditions degrowth in a population can increase survivorship and thus residual reproductive capacity. Fourthly, although there do exist some density-dependent controls of fecundity (see, for example, Eversole, 1974, summarized in Russell-Hunter, 1978), in most cases bivalve and gastropod populations show a reproductive output that is proportional to trophic input. For several species of freshwater snails, comparative studies have demonstrated this relationship to hold true (McMahon et al., 1974; Calow, 1978, 1979). Fifthly, detection of any endogenous senescence is prevented by the fact that the majority of populations of aquatic bivalves and snails exhibit an environmental cutoff at a certain size. This maximum size may be equivalent to a certain age, but only for that specific population. Sometimes these cutoff sizes can be correlated with allometry in the growth of structures for respiratory exchange (surface:mass ratio changes), or to impinging velocities in streams, or to certain trophic features. Differential mortality, whether abiotic or biotic, can often be related to seasonal changes in the abiotic environment. In broad terms, mortality like maturation is a facultative process in these molluscs.

Great plasticity of molluscan patterns of growth and of life-cycles (Russell-Hunter, 1961, 1978; Calow, 1978, 1983) result from these five characteristic "indeterminate" features. The adaptive advantages of heritable capacity for all five features, and the probablility that they have been linked in evolution, are obvious intuitively, although testable quantification of either postulate may take rather more effort.

If capacity for degrowth has been packaged with these other features of interdeterminate growth in evolution, this has some broader implications for phyletic relationships. For those biologists who hold that a phyletic connection between the Mollusca and the turbellarian-rhynchocoel stock is more likely than any other (Yonge, 1947; Morton and Yonge, 1964; Russell-Hunter and Brown, 1965; Russell-Hunter, 1979, 1982; Seed, 1983) degrowth can be regarded as a common archetypic feature, retained from the flatworm-stem in the bivalves and gastropods, but not in the more highly-evolved cephalopods. Although the discovery of a living monoplacophoran, *Neopilina,* in 1952 reopened discussion of possible metamerism in ancestral molluscs, it is clear that true metameric segmentation, as found in the phyla Annelida and Arthropoda, never occurs in the Mollusca. In particular, Russell-Hunter and Brown (1965) clearly demonstrated that the multiplied structures of chitons show none of this metamerism, either as serial sets of organs or in their morphogenesis. More recently, Soviet functional morphologists (Minichev and Sirenko, 1984) have confirmed and extended these observations on chitons and accepted our view of their phyletic significance.

Developmental evidence, including patterns of early cleavage and the initial types of free-living larvae, which also is claimed to link molluscs with the annelid-arthropod phyla rather than with the flatworms, is similarly suspect. The late Donald P. Costello emphasized that the occurrence of spiral cleavage has no obvious significance in the interrelationships of animal phyla (Costello and Henley, 1976). There are three main categories of cleavage (radial, bilateral, and spiral), and three basic types of spiral cleavage (by quartets, by duets and by monets); while for most animal embryos these spiral categories inevitably become modified into bilateral cleavage at some later stage in development (Costello, 1948, 1955). Cleavage is a dynamic process in time and spiral cleavage is not absolutely correlated with mosaic development. A grand-scale division of the invertebrate phyla into the "spiralia" and the deuterostome-rest could only be seriously proposed by a zoologist ignorant of the variety of cleavage patterns (Costello and Henley, 1976; Russell-Hunter, 1979).

The capacity for degrowth in flatworms and molluscs may involve controls of genetic expression which cannot coexist with those involved in any morphogenesis which produces a serial succession of segments, each containing unit subdivisions of the several organ systems, as in the "budding" development of true metameric segmentation (in the phyla Annelida and Arthropoda). Some molecular biologists, whose view is that ageing in higher animals results from the accumulation of defects in macromolecules through errors in synthesis (Kirkwood, 1977; Kirkwood and Holliday, 1979), correlate the absence of endogenous senescence in certain organisms with indeterminate growth patterns. The controls for metameric development, which at the molecular level are possibly neurohormonal or even JH-like, may well prove to mandate those particular differentiations by selectively switching on certain sets of genes in some irrevocable fashion which is incompatible with the capacity for degrowth exhibited by molluscs and flatworms. Parenthetically, in this matter of incongruent controls involved in morphogenesis, the case of the phylum Rhynchocoela or Nemertea is particularly interesting. The incompatibility hypothesized here would suggest that nemertean retention of capacity for degrowth and dedifferentiation-rejuvenation involved the group in the costs of all the mechanical inefficiences subsumed in great length *without* segmentation. At least as regards the Mollusca, the retained capacity for degrowth is closely associated with the facultative features of other four parameters of life-history as set out above, and with extensive interpopulation plasticity in life-cycles. Together, these features provide yet another kind of functional evidence illustrating the phylogenetic absurdity of linking the molluscs with the Annelida-Arthropoda phyla in a so-called subkingdom Protostomia or Spiralia.

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RENAL ADAPTATIONS OF PROSOBRANCHS TO THE FRESHWATER ENVIRONMENT

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ABSTRACT

Following brief reviews of the reduced diversity of freshwater prosobranchs compared with marine forms, and of the basic processes of kidney function in gastropods, the adaptations of renal processes in freshwater prosobranchs, principally Viviparacea and Neritacea, are related to osmoregulatory problems.

Mechanisms by which a high flow rate of urine is maintained are explained in terms of the anatomy of the filtration sites, the physiology of the filtration process, and the mechanics of fluid flow through the renal system. It is concluded that the development of muscular pumping in the kidneys of freshwater prosobranchs is of considerable significance. The reabsorption of ions and metabolites is considered in terms of the effectiveness of processes in the pericardial cavity, the kidney, the ureter and other pallial additions to the kidney, and finally the epithelium of the mantle cavity. Salt absorption by the gill could be important.

Freshwater gastropods face one major osmoregulatory problem: how to excrete very large volumes of water while retaining or absorbing ions and metabolites. The means employed by freshwater prosobranchs in these directions forms the main subject of this paper, but before considering this directly I would like to point out how few prosobranch families there are in fresh water. Table 1 summarises the present-day situation, from which it can be seen that only 10 families are found in fresh water. In contrast, there are over 100 in the sea. Of the freshwater groups, the Cerithiacea have radiated most widely in the ancient freshwater lakes such as Lake Tanganyika and Lake Baikal (Boss, 1978), but we know very little of their physiology or ecology. The Rissoacea are widespread, but are mostly very small, and as with the Valvatacea this has meant that very little physiological information is available. This leaves us with the Viviparacea and Neritacea as the only groups that we know much about, and I will perforce have to concentrate on them. This is not to say that other freshwater prosobranchs have not solved their osmoregulatory problems in quite different ways, and there is a field here wide open for investigation, using modern micro-analytical techniques.

The basic organisation of molluscan excretory systems is now well established (e.g. Potts, 1975; Martin, 1983), and the processes involved in urine production can be illustrated by reference to one particular renal system, that of *Viviparus* (Fig. 1). Ultrafiltration of the blood occurs across the heart wall, usually the auricle. The ultrafiltrate collects in the pericardial cavity, and then moves through the renopericardial canal into the kidney, where ions and water are reabsorbed. Urine is usually excreted into the mantle cavity, where further reabsorption may occur; but occasionally, as in *Viviparus,* it is taken to the end of the mantle cavity in a pallial ureter which is also involved in reabsorption. Although there has been some discussion of the reality of the ultrafiltration process in bivalves (e.g. Tiffany, 1972; Potts, 1975; Mangum and Johansen, 1975), and it does not occur in terrestrial pulmonates (Vorwohl, 1961; Skelding, 1973), it is probably universal in prosobranchs.

Freshwater prosobranchs face the problem of potentially large rates of water inflow due to osmosis, and the problem of loss of salts from the body by diffusion. In general they cope with these two problems by increasing the rate of urine production while at the same time increasing the rate of absorption of salts, both from the urine and from the external medium (Burton, 1983). The rates of urine flow may be 10 to 20 times higher in freshwater prosobranchs than in marine species (see Table 2). Unfortunately, however, very few figures are available, and although the rates for freshwater prosobranchs are reasonably consistent, those for marine prosobranchs themselves differ by an order of magnitude. Only the very large marine prosobranchs have been investigated, and we need many more measurements of urine production rates in a variety of snails before making valid generalisations. There is, however, no doubt about the hypo-osmotic nature of urine in freshwater prosobranchs (Table 3).

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Table 1 Freshwater prosobranchs and their relatives.

Brackish water	*Fresh water*	*Terrestrial*
	ORDER NERITACEA	
	SUPERFAMILY NERITACEA	
Neritidae	Neritidae	Helicinidae
		Hydrocenidae
	ORDER MESOGASTROPODA	
	SUPERFAMILY VALVATACEA	
—	Valvatidae	—
	SUPERFAMILY VIVIPARACEA	
—	Viviparidae	"Cyclophoridae"
		Ampullariidae
	SUPERFAMILY RISSOACEA	
Hydrobiidae	Hydrobiidae	Hydrobiidae
Rissoidae	Bithyniidae	Aciculidae
Assimineidae		Assimineidae
	SUPERFAMILY CERITHIACEA	
Cerithiidae	Melaniidae (= Thiaridae)	—
Melanopsidae	Pleuroceridae	
etc.	Syrnolopsidae	
	Melanopsidae	

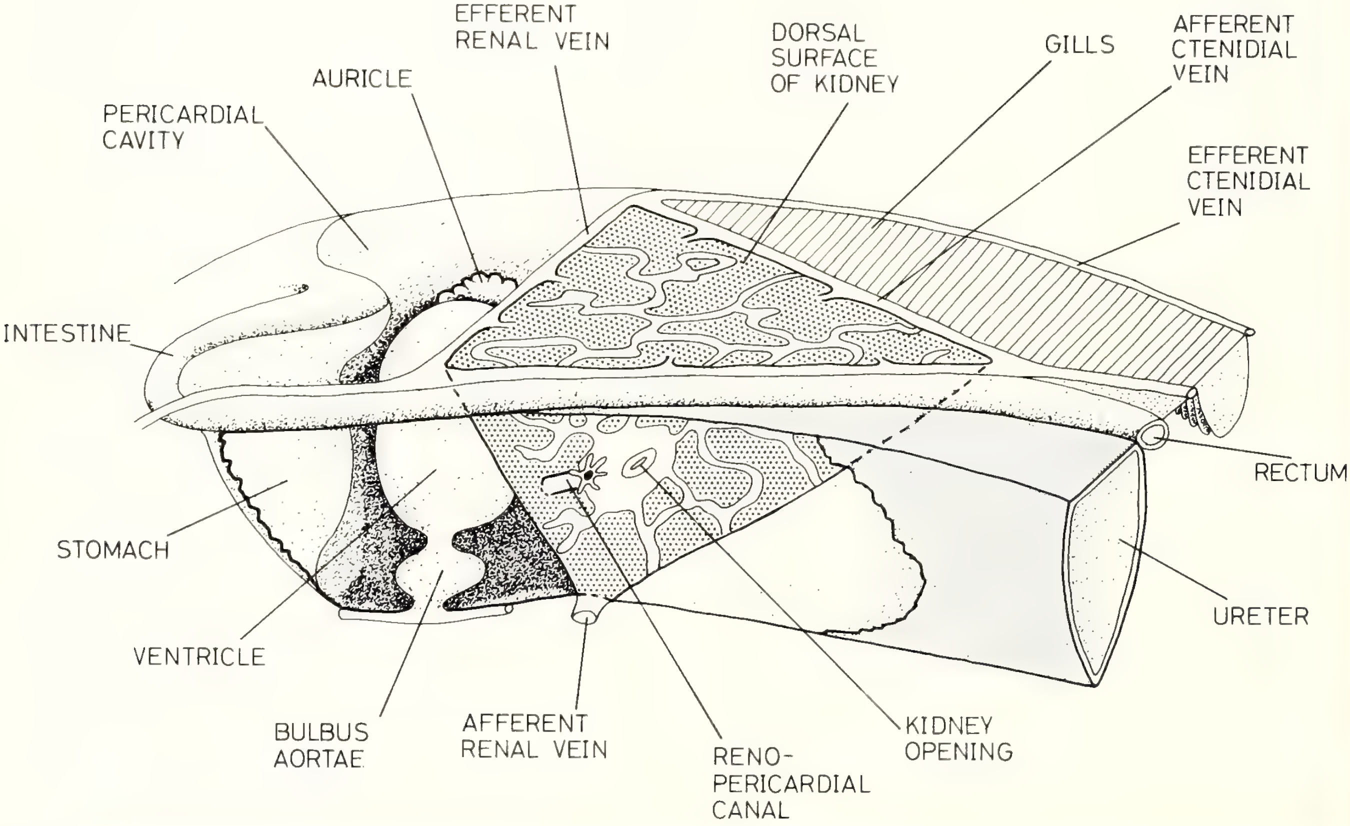

EFFERENT RENAL VEIN
AURICLE
PERICARDIAL CAVITY
DORSAL SURFACE OF KIDNEY
GILLS
AFFERENT CTENIDIAL VEIN
EFFERENT CTENIDIAL VEIN
INTESTINE
RECTUM
STOMACH
URETER
VENTRICLE
BULBUS AORTAE
AFFERENT RENAL VEIN
RENO-PERICARDIAL CANAL
KIDNEY OPENING

Fig. 1. Diagram of the excretory system of *Viviparus* seen from the right side. The ureter is shown with part of the right wall removed, and the roof and right wall of the pericardial cavity are shown as if transparent. Not to scale. Partly after Little (1965b) and Andrews (1979).

Table 2. Rates of urine production in marine and freshwater prosobranchs.

	Tissue weight g	Temperature °C	Urine production µl/g/min Range	Mean	Reference
MARINE SPECIES					
Haliotis rufescens	390–1300	12–14	0.1 –0.35	— [1]	Harrison, 1962
Strombus gigas	240–350	22	0.04–0.07	0.05[2]	Little, 1967
FRESHWATER SPECIES					
Viviparus viviparus	0.6–2.6	19	0.14–0.37	0.25[1]	Little, 1965b
Viviparus viviparus	0.9–1.7	19	0.64–1.27	0.91[2]	Little, 1965b
Viviparus malleatus	15.4–25.1	—	—	0.70[1]	Monk and Stewart, 1966
Pomacea lineata	27–29	25	0.50–1.14	0.96[3]	Little, 1968

[1] Measured by cannulation. [2] Measured by use of inulin. [3] Fluid taken from the mouth of the shell.

Table 3. Osmotic pressure of blood and urine in freshwater prosobranchs.

Species	Osmotic pressure (mOsm/kg ± SE) BLOOD	URINE	Reference
Neritina latissima	90.4 ± 2.5	57.4 ± 5.1	Little, 1972
Viviparus viviparus	68.1 ± 2.0	13.6 ± 2.2	Little, 1965b
Pomacea lineata	117.4 ± 3.1	27.4 ± 3.3	Little, 1968
Potamopyrgus jenkinsi	52	43	Todd, 1964

While *Viviparus* and *Pomacea* have been shown to produce urine with an osmotic pressure about 20% of that of the blood, the urine of *Neritina* and *Potamopyrgus* shows values of 60–80% of that of the blood. It is possible that these differences reflect sampling difficulties rather than genuine differences, and again the investigation of a wider variety of species would be of great interest.

On the assumption that freshwater prosobranchs deal with their osmotic problems in the main by producing high rates of flow of hypo-osmotic urine, most of this paper will consider how their renal systems are adapted for the apparently contradictory purposes of high flow rate and increased salt absorption.

HIGH FLOW RATE OF URINE

This has two components which are quite separate from each other: an increase in the rate at which the ultrafiltrate is produced, and an increase in the rate at which fluid flows through the renal system. These two components will be considered in turn.

HIGH FILTRATION RATE

Ultrafiltration across the wall of the heart takes place mostly in the auricle, which is relatively thin walled. In some gastropods there is evidence for some filtration across the wall of the ventricle (e.g. Andrews and Little, 1972), but this appears to be rare (Andrews, 1981). The pressure system involved in the ultrafiltration process has not yet been elucidated in detail, but the constant-volume ideas of Ramsay (1952) and Krijgsman and Divaris (1955) have been developed by Andrews (1979). She suggested that initial filtration in monotocardians normally occurs through partially isolated compartments of the auricle under a high auricular pressure. This filtrate is usually trapped in filtration chambers formed of squamous epithelial cells, but is then released from the chambers as pericardial pressure falls below that of the auricle. Figure 2 shows in diagrammatic form the organisation of the auricle surface. The filtration site itself is probably the basement membrane, but fluid passes through this membrane only where the podocytes leave gaps (the filtration slits) between the pedicels. Fluid in the filtration chambers reaches the pericardial cavity through extracellular channels in the podocytes.

How is this system adapted in freshwater prosobranchs to provide a greater rate of filtration than in marine forms? The answer has been provided in only two cases. The first is that of *Viviparus* spp., where the *area* of podocytes is much increased compared to the area found in marine forms such as *Littorina*. In *Littorina littorea,* relatively small filtration pouches occur, mostly in a restricted part of the auricle facing the reno-pericardial canal (Andrews, 1976a, 1981). In *Vivi-*

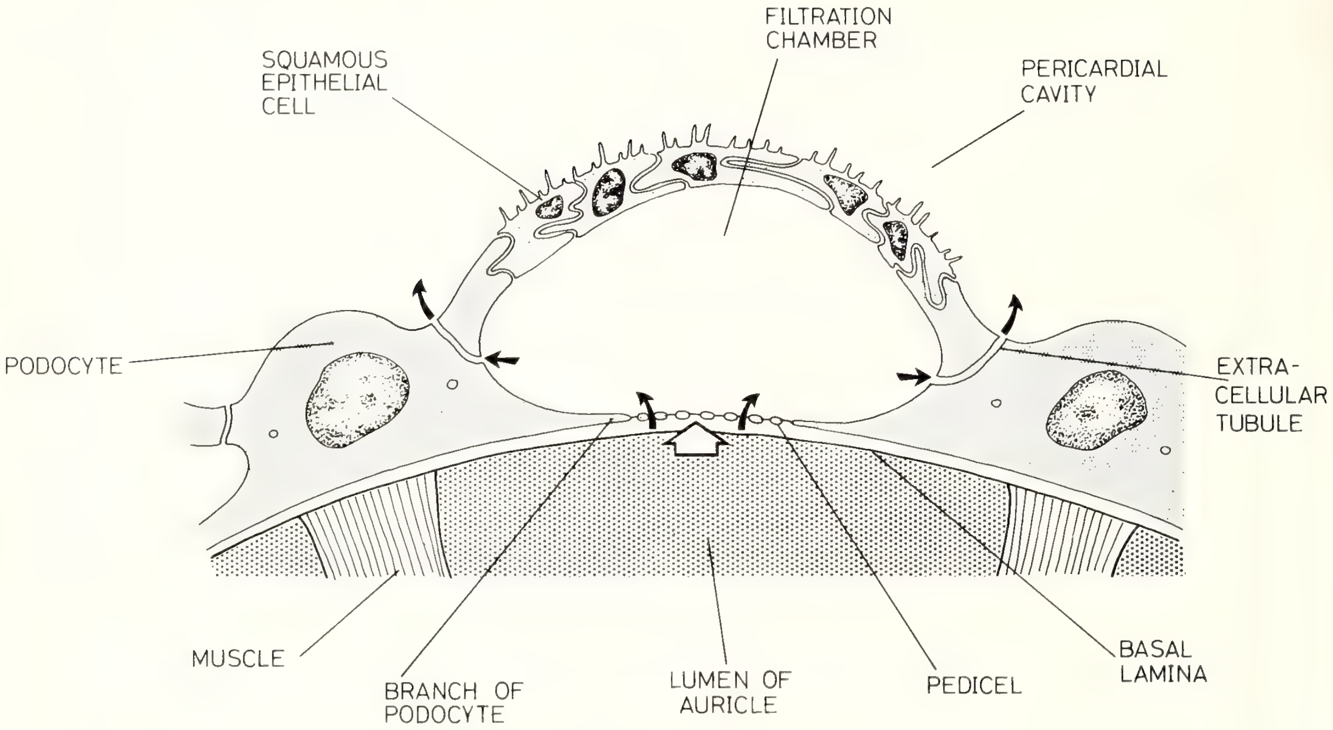


Fig. 2. Diagram of the filtration site in a monotocardian prosobranch auricle. The open arrow shows the site of filtration. Black arrows show the route of the ultrafiltrate to the pericardial cavity. Not to scale. Partly after Andrews (1981) and Boer et al. (1973).

parus spp., similar filtration pouches overlying podocytes cover most of the surface of the auricle (Andrews, 1979, 1981). The greater area of filtration sites presumably allows higher rates of filtration. The second case investigated is the pilid *Marisa cornuarietis,* in which the epicardium over the auricle consists *not* of podocytes with squamous cells overlying filtration pouches, but of cells which are permeated by extra-cellular channels but have no overlying filtration pouches. Filtered fluid in this case therefore passes only through the extra-cellular channels in these cells to reach the pericardial cavity. The cells are much more robust than the delicate podocytes of other prosobranchs. Andrews (1976b, 1981) has suggested that podocytes have been replaced in this situation because greater mechanical strength was needed: the heart of pilids is more active and muscular than that of viviparids, and epicardial cells must withstand the greater movement. Whatever the explanation, it is evident that in the only two examples to be investigated in detail, the adaptations of the prosobranch filtration sites are quite different. Before making any generalisations, we need to know about structural diversity in a variety of freshwater prosobranch families.

Whatever the structure of the filtration sites, however, the second major variable to be considered is the amount of filtration pressure applied to the sites. The rate of filtration will be determined by the excess of hydrostatic pressure over the colloid osmotic pressure of the blood (see, e.g. Potts, 1975). From the work of Andrews (1979, 1981), it can be concluded that this is determined partly by the changing balance of hydrostatic pressures in the auricle and the pericardial cavity during the heart-beat cycle, and partly by the architecture of the heart and the degree to which the filtration sites are isolated from the main chamber of the auricle during auricular systole. Very little is known about the details of hydrostatic pressure distribution in the blood systems of prosobranchs. Some figures are available for the marine archaeo-gastropods *Haliotis corrugata* (Bourne and Redmond, 1977) and *Patella vulgata* (Jones, 1970), for the freshwater pulmonate *Lymnaea stagnalis* (Dale, 1974) and for the terrestrial pulmonate *Helix pomatia* (Jones, 1971; Sommerville, 1973). In all these examples, the maximum difference between hydrostatic pressure in the auricle and in the pericardial cavity has been recorded as being of the order of 1–2 cm H_2O. Studies on the terrestrial pulmonates *Deroceras reticulatum* and *Limax pseudoflavus* (Duval, 1983), using more sophisticated techniques have, however, recorded pressure differences across the auricle wall at systole of the order of 20–50 cm H_2O. To calculate filtration pressure we also need to know the colloid osmotic pressure of the blood, and for this also there is very little information. Only in the marine prosobranch *Buccinum undatum* has this been measured directly (Mangum and Johansen, 1975), and in this case it was equivalent to about 1 cm H_2O. In summary, therefore, we have no clear picture of the pressures involved in filtration in either marine or freshwater prosobranchs. If we add to this the problem that the pressure at the filtration sites may differ from that in the auricular lumen, it is obvious that we are as yet in no position to assess the situation. It seems quite possible that filtration pressures are higher in freshwater forms than in marine ones, but this is a hypothesis that is still to be tested.

HIGH RATE OF FLOW THROUGH THE KIDNEY

Filtrate from the pericardial cavity reaches the kidney via the renopericardial canal, and if a high flow rate of urine is to be achieved, the high rate of filtration must be accompanied by the rapid processing of the filtrate in the kidney. Because this involves the reabsorption of salts and metabolites (which I shall consider later), flow through the kidney consists not just of entry, passage through and exit, but the distribution of fluid throughout the kidney's interstices. In all monotocardians, the renopericardial canal is ciliated, with cilia beating towards the kidney lumen, and it incorporates a muscular sphincter. The kidney pore, opening to the mantle cavity or to a pallial ureter, also incorporates a muscular sphincter.

In most marine monotocardians, such as *Littorina* spp., ciliated cells are abundant lining the kidney lumen, and these may be the effective circulatory agents. However, it should also be noted that the outer surface of the kidney usually contains some muscular elements beneath the epithelial cell layer (see, e.g. Perrier, 1889; Fretter and Graham, 1962; Delhaye, 1974), and these elements could conceivably play some part in contracting or expanding the kidney.

In the freshwater prosobranchs so far examined, the situation is quite different. In *Viviparus viviparus*, the kidney does contain cells with cilia, but muscle fibres are also prominent throughout the spongy walls of the kidney (Andrews, 1979). Observations of the kidney *in vitro* suggest that muscular action is the main effector in moving fluid into, around and out of the kidney (Little, 1965b). As the kidney muscles contract, so the excretory pore opens and a pulse of urine is forced into the ureter. The excretory pore then closes, the sphincter of the renopericardial canal opens, and the kidney slowly expands as filtrate flows in from the pericardial cavity. Because the kidney has a sponge-like structure, this incoming fluid is distributed throughout the complicated interstices of the kidney lumen.

In the freshwater Ampullariidae, the true kidney (formerly called the posterior chamber of the kidney) is not involved in salt and water transport (Little, 1968), and the contents are probably circulated by cilia (Andrews, 1965). The pallial ureter (formerly called the anterior chamber of the kidney; see Andrews, 1981 and Demian and Yousif, 1973) is responsible for salt reabsorption (Little, 1968). This organ is well supplied with muscle fibres (Andrews, 1965; 1976b), and observations *in vitro* showed it to be strongly contractile (Little, 1968). Since the urine is released in pulses as it is in *Viviparus*, it seems probable that the contractions of the pallial ureter provide the driving force moving fluid through the renal system. This system is analogous to that in *Viviparus*, but must have evolved separately because while the kidney of *Viviparus* represents the nephridial gland of marine ancestors, the contractile organ in Ampullariidae is pallial in origin (Demian and Yousif, 1973).

The adoption of a muscular system to move fluid through the renal system allows freshwater prosobranchs to excrete fluid at a faster rate than marine forms, which seem to use cilia. It probably also allows greater control of fluid movement. We know almost nothing of the mechanisms involved, but preliminary observations on *Viviparus* (Little, 1965b) showed that while changes in the volume of fluid in the pericardial cavity altered the volume and frequency of pulses of urine expelled from the kidney, volume and frequency showed an inverse relationship, and overall rate of urine flow was unchanged. On the other hand, changes in hydrostatic pressure of the blood greatly changed the overall rate of urine production, suggesting a feedback mechanism controlled by pressure sensors. Andrews (1979) has pointed out that the auricle, the opening of the renopericardial canal and the kidney pore in *Viviparus* are all richly innervated by branches from the visceral ganglion, so that a feedback circuit may link all three sites.

Although the development of a muscular system controlling fluid flow is important in the Viviparidae and the Ampullariidae, it is likely that entirely different strategies have been adopted by other freshwater families. We know nothing about such matters in the Neritidae, Valvatidae, Hydrobiidae, Bithyniidae or Melaniidae, although Delhaye (1974, 1975) has described the general histology of kidneys in some of these families. A muscular system is unlikely to be present in the Hydrobiidae, since in the only species to be investigated, *Potamopyrgus jenkinsi*, the kidney consists of a large cavity ramifying between the viscera (Delhaye, 1975). Both experimental and structural investigations of a wide variety of freshwater families are essential to establish the range of strategies found in fresh water.

REABSORPTION OF IONS AND METABOLITES

Four possible regions may contribute to reabsorption from the primary ultrafiltrate or may compensate for loss of ions from the body by diffusion.

PERICARDIAL CAVITY

The ionic composition of pericardial fluid has been measured in only very few marine and freshwater prosobranchs. In the marine mesogastropod *Strombus gigas*, K^+ is raised in concentration by 2.5 mM/l and Ca^{++} lowered in concentration by 1.1 mM/l in the pericardial cavity (Little, 1967), but other ions are at the same concentration as in the blood. In the freshwater neritacean *Neritina latissima*, both osmotic pressure and chloride concentration are the same in pericardial fluid as in the blood (Little, 1972). In *Viviparus viviparus* and *Pomacea lineata* the osmotic pressure and concentrations of all ions are the same in blood and pericardial fluid except for the lowered calcium concentration (by 1.0 mM/l in *Viviparus* and 4.6 mM/l in *Pomacea*) in pericardial fluid (Little, 1965b, 1968). The similarity of composition of pericardial fluid with that of blood is thought to be due to its origin as an ultrafiltrate of the blood, and the lowered calcium concentration in pericardial fluid is probably due to the fact that some calcium is bound to protein, and little protein passes across the heart wall. There is no suggestion that the pericardium of freshwater prosobranchs is adapted for the reabsorption of ions.

The only evidence pointing to reabsorption in the pericardial cavity is that of Andrews (1979) and Little (1979) for *Viviparus*. Andrews showed that the epicardium of the ventricle has the characteristics of cells concerned with active transport: extensive basal infoldings associated with mitochondria, and long apical microvilli. The cells also have large glycogen deposits. Little (1979) has shown that the pericardial fluid contains only 5% of the glucose concentration of blood. It seems likely, therefore, that the epicardium of the ventricle is responsible for this reabsorption. Unfortunately there is no information to allow comparison with marine forms, but it is likely that reabsorption of glucose and other nutrients very early in the process of urine formation might be an adaptation to freshwater life, where urine flows rapidly through the renal system.

KIDNEY

The kidneys of marine prosobranchs are not, so far as is known, important in the reabsorption of ions from the ultrafiltrate that passes to them from the reno-pericardial canal (Potts, 1975). In *Strombus gigas* and *Nerita fulgurans,* ion concentrations in kidney fluid are essentially the same as those in the blood (Little, 1967; 1972). In *Littorina littorea* the same statement applies, but there is reabsorption of *ca.* 2 mM/l of SO_4^{--} in the kidney (Rumsey, 1971). Overall, the picture in marine gastropods is of very slight modification to the ionic composition of the ultrafiltrate by the kidney.

Information on reabsorption of organic molecules in the kidneys of marine gastropods is confined to the archaeogastropod *Haliotis rufescens,* in which glucose concentrations in the left kidney were lower than in the blood (Harrison, 1962). This was not so in the right kidney, so that glucose reabsorption must have taken place in the left kidney and not within the pericardial cavity.

One of the greatest differences found in freshwater gastropods is the ability to reabsorb ions in the kidney, producing hypo-osmotic urine, as already emphasised in Table 3. This reabsorption concerns mainly the ions Na^+ and Cl^-, since these account for a large proportion of the osmotic pressure. Similar proportions of K^+ and Ca^{++} are also reabsorbed (Table 4), and the low osmotic pressures seen in the final urine of some species (Table 3) suggest that some reabsorption of other component ions such as HCO_3^- probably occurs.

In *Viviparus,* this absorption is probably carried out by mucoid cells which, as well as secreting a mucoprotein or neutral polysaccharide, have very extensive basal infoldings associated with long mitochondria (Andrews, 1981). This type of cell is found *only* in the nephridial gland of marine intertidal prosobranchs, but is the predominant cell type in the kidney of *Viviparus*. From this it may be suggested that it is the expansion of the nephridial gland that has given *Viviparus* the ability to reabsorb salts at such a high rate. In *Pomacea,* mucoid cells that are also reabsorptive are not found in the kidney, and reabsorption is carried out in the pallial ureter. In freshwater Neritidae we have no fine-structural observations, but the light-microscope work of Delhaye (1974) showed that the kidney has cells with fine basal striations (which are probably basal infoldings) as well as mucoid cells.

We know nothing about other freshwater species apart from Delhaye's (1975) light-microscope descriptions for Hydrobiidae, Bithyniidae and Melaniidae. It is impossible to correlate these with Andrews' (1981) classification of cell types based on observations with the electron microscope, although it is apparent that all 3 families have reabsorptive cells. Examination of the renal physiology and fine structure of these families could broaden our thinking about both the function and evolution of freshwater kidneys. In particular, it could provide insight into how kidneys that are specialised for ion reabsorption have evolved from those that reabsorb essentially only organic metabolites.

PALLIAL REABSORPTION

In several freshwater families, organs of pallial origin are involved in ion reabsorption. In *Viviparus,* a ureter takes fluid to the end of the mantle cavity, and from the ureter a small amount of salt, together with some water, is reab-

Table 4. *Urine: blood ratios for ions in freshwater prosobranchs.*

Species	*U/B ratios*				*Reference*
	Na^+	*K^+*	*Ca^{++}*	*Cl^-*	
Viviparus viviparus	0.28	—	0.26	0.34	Little, 1965b
Pomacea lineata	0.50	0.50	0.28	0.42	Little, 1968
Neritina latissima	—	—	—	0.57	Little, 1972

sorbed (Little, 1965b). The reabsorptive cells, characterised by deep basal infoldings associated with mitochondria, are also packed with glycogen (Andrews, 1979).

In the Ampullariidae, the modified pallial epithelium forms an analogue of the kidney in *Viviparus,* with plate-like lamellae composed almost entirely of reabsorptive cells (Andrews, 1976b).

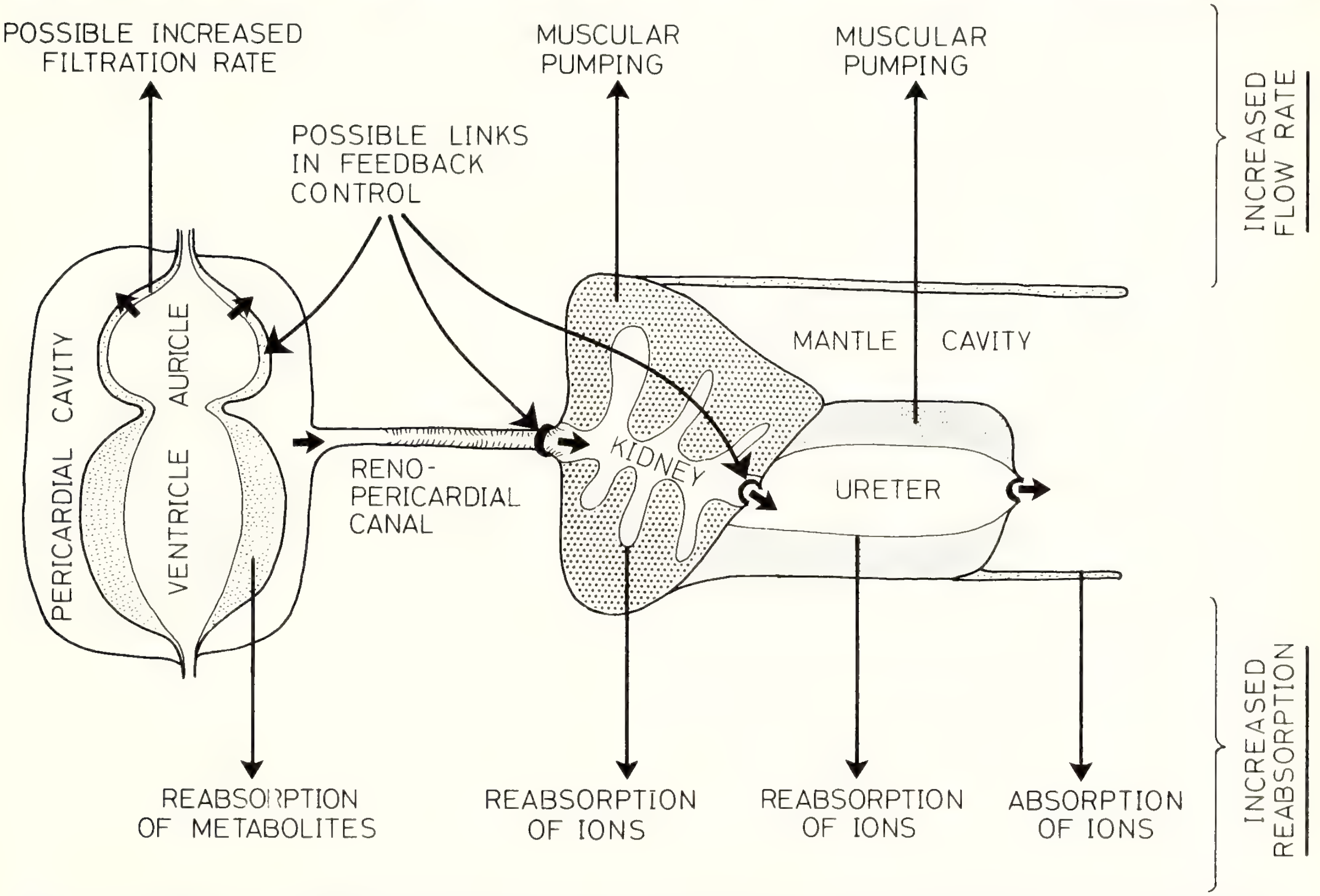
In freshwater Neritidae, it has been suggested that ions are reabsorbed as urine passes through the mantle cavity (Little, 1972). This suggestion raises the possibility that reabsorption may occur in the mantle cavity in some or all freshwater prosobranchs. It therefore leads on to the last section of this paper which considers the absorption of salts outside the renal system (see also Little, 1981).

EXTRA-RENAL SALT ABSORPTION

As long ago as 1939, Krogh showed that *Viviparus* could take up chloride from very dilute solutions. Each freshwater species has, in fact, an external concentration at which it reaches equilibrium for each ion. In *Marisa cornuarietis,* the rate of calcium uptake fell when external calcium was lower than about 1 mM/l, and 0.6 mM/l was regarded as "sub-optimal" by Meier-Brook (1978), although snails could grow and reproduce at this concentration. For *V. viviparus,* the minimum equilibrium concentration for calcium was 0.2 mM/l, while for sodium the value was 0.006 mM/l (Little, 1965a). Many pulmonates can survive at much lower concentrations, especially in relation to calcium. In *Lymnaea stagnalis,* for instance, calcium uptake can take place from 0.06 mM/l (Greenaway, 1971). The equilibrium values are probably important in governing the distribution of snails in hard and soft waters (Little, 1965a).

The observations of salt uptake suggest that there must be salt-absorbing cells somewhere in the epidermis, and probably in the mantle cavity. Krogh (1939) did not speculate about their position, and I know of no work that has located cells taking up chloride in gastropods. Sen Gupta (1977) has demonstrated the presence of ionic calcium and of alkaline phosphatase in the gills of *V. bengalensis.* By analogy with the gills of other groups such as crustaceans and teleosts, the gill seems the most likely place for uptake. Future workers might do well to investigate the potential of the molluscan gill in this direction.

This review has not considered the possibility of the food as a source of inorganic ions. In freshwater pulmonates,


POSSIBLE INCREASED FILTRATION RATE
MUSCULAR PUMPING
MUSCULAR PUMPING
INCREASED FLOW RATE
POSSIBLE LINKS IN FEEDBACK CONTROL
PERICARDIAL CAVITY
AURICLE
VENTRICLE
RENO-PERICARDIAL CANAL
KIDNEY
MANTLE CAVITY
URETER
INCREASED REABSORPTION
REABSORPTION OF METABOLITES
REABSORPTION OF IONS
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ABSORPTION OF IONS

Fig. 3. Diagram of the sites in the kidney of freshwater prosobranchs that are important in increasing rates of urine flow and in increasing rates of reabsorption of salts and metabolites.

food supply may account for a significant percentage of the snail's calcium input (see, e.g. Young, 1975, for discussion). Such could also be the case for freshwater prosobranchs, but I know of no investigation on this subject.

CONCLUSIONS

The freshwater prosobranchs so far investigated, mainly in the families Viviparidae, Ampullariidae and Neritidae, have increased the flow rate of fluid through the renal system, and the rate of reabsorption of salts, in comparison with marine groups. In Fig. 3 the sites at which these modifications occur have been outlined. Muscular pumping may take place in either the kidney or the pallial ureter, while increased reabsorption of ions occurs in both. The scheme proposed in Figure 3 should not, however, hide the fact that we know almost nothing about renal strategies found in other freshwater prosobranchs. In the families Valvatidae, Hydrobiidae, Bithyniidae and Melaniidae the strategies adopted may be entirely different, and a study of renal physiology and fine structure in these groups would be of the greatest interest.

ACKNOWLEDGEMENTS

I am grateful to Dr. E. B. Andrews and Dr. T. E. Thompson for their comments on this paper.

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IONIC REGULATION IN FRESHWATER MUSSELS: A BRIEF REVIEW

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ABSTRACT

Freshwater bivalves are subject to salt loss to the environment and the osmotic uptake of water. Although the gradient for water movement is low due to the reduced blood osmolality (45–60 mOsm), water influx in molluscs may be substantial since they have the highest renal filtration rates of freshwater animals. The rate of salt transport in freshwater unionid mussels is similar to other freshwater animals (1–2 μmol (g dry tissue · hr)$^{-1}$). In contrast, salt turnover in corbiculid bivalves is 5–10 times greater.

In studies on the mechanism of Na transport, we observed a coupled cation exchange (H, NH_4) and Cl transport is coupled to base (HCO_3 or OH) exchange. Thus, salt transport is intimately linked to acid-base balance. Although freshwater mussels present a large epithelial surface to the environment (gills, mantle, foot), we have found that the gills account for most of the Na and Cl uptake in Unionids.

Recently, we have shown that Na transport 'but not Cl) is stimulated 200% by a variety of biogenic "monoamines," including serotonin, when injected into the intact animal. In the isolated gills, serotonin, cyclic AMP and theophylline are effective in increasing Na influx. Bivalve gill tissue contains a serotonin sensitive adenylate cyclase system which may be involved in regulating Na transport. In addition, Na transport in freshwater mussels is inhibited by prostaglandins (PGE_2) presumably derived from the arachidonic acid present in gill tissue phospholipids.

Calcium is a major cation in freshwater mussel blood; second only to Na in pondwater acclimated animals. Calcium is abundant in the shell and in calcium concretions widely distributed in various tissues. The gills contain abundant Ca concretions, accounting for 25–50% of the dry mass. Under conditions of hypoxic stress, we have noted a reciprocal relationship between blood Na and Ca. When Na is lost from the blood, Ca usually increases and may become the principal cation. The source of Ca may be from the shell since the gill concretions were observed to increase in mass, apparently serving as Ca deposition sites.

In recent studies we have noticed a correlation between Na influx and net Ca loss from mussels. These data suggest a Na/Ca exchange mechanism involved in ionic regulation. In separate studies, we have noticed that Ca concretions disappear from the gills of gravid females during the time of shell formation in developing embryos. These data suggest the developing bivalve larvae may be obtaining "mineral nutrition" directly from the adult.

The freshwater bivalves maintain body fluid solute concentration 25–50% of that found in other freshwater animals (Krogh, 1939; Potts, 1954; Prosser, 1973; Dietz, 1977; 1979; Deaton, 1981; Burton, 1983). In addition, the specific ion concentrations in clam blood are not usually a simple dilution of body fluids since Ca and HCO_3 are typically major solutes in addition to NaCl. Although mussels have a lower solute concentration and osmotic gradient, they experience the same problems as other freshwater animals: gaining water osmotically and losing solutes by diffusion and excretion. Estimates of urine production from renal clearance of inulin or polyethylene glycol is 20–50 ml/Kg · hr (Potts, 1954; Murphy and Dietz, 1976; Dietz and Branton, 1979) which is higher than other freshwater animals (Kirschner, 1967; Prosser, 1973) and suggests that mussels have a high turnover of water even though the osmotic gradient is extremely low.

Despite the high water turnover and lower salt concentration, the freshwater unionids have salt transport rates remarkably similar to other freshwater animals. Thus, freshwater bivalves can maintain hydromineral balance in dilute media (Dietz, 1977; 1978; 1979). Salts lost across permeable epithelia and in the urine are offset by ions accumulated by epithelial transport. In our earlier studies, we showed that Na and Cl uptake occur by independent saturable pro-

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cesses (Fig. 1). The influx of Na or Cl in unfed unionids is about 1–2 μmol (g dry tissue · hr)$^{-1}$ with a transport affinity of about 0.1 to 0.2 mM/l (Dietz, 1978; Dietz and Branton, 1979). In contrast, the corbiculids transport salt 5–10 times faster than unionids and the fluxes are more characteristic of brackish water animals (Prosser, 1973; McCorkle and Dietz, 1980).

ION TRANSPORT

In earlier studies, investigators concentrated on characterizing the ionic and osmotic regulation in intact freshwater mussels (Krogh, 1939; Hiscock 1953; Chaisemartin et al., 1968; Dietz, 1979; Deaton, 1981). A major theme of our studies with the freshwater bivalves has been the independence of Na and Cl transport and the coupled cation and anion exchanged. An attractive hypothesis which has considerable supporting evidence is the coupling of ion balance with acid/base balance (see Kirschner, 1982). More recently, we have been exploring the role of Ca in Na transport. It should be noted that Na balance must occur whether or not the animal is in acid/base balance. Thus, strict coupling between Na and H could be detrimental to the animal's survival and other mechanisms must contribute to Na balance under stressful conditions.

Sodium transport in bivalves occurs in exchange for endogenous cations. We have reported an extensive Na/H and Na/NH$_4$ exchange and recent evidence suggests a Na/Ca antiport system as well. Chloride uptake is by a Cl/HCO$_3$ or Cl/OH exchange mechanism. We have partitioned the unidirectional fluxes into the various components: active transport, diffusion and exchange diffusion (see Ussing, 1949) (Table 1). Active transport is the principal component of Na influx with diffusion and Na/Na exchange diffusion being virtually non-existent in the unionids (Dietz, 1978). However, in the corbiculids exchange diffusion accounts for 67% of the ^{22}Na turnover in pondwater acclimated mussels (McCorkle and Dietz, 1980). Following salt depletion active transport accounts for 45% of the ^{22}Na turnover and exchange diffusion is reduced to 50% in *Corbicula fluminea.* Chloride isotope turnover in the unionids, however, may be up to 90% exchange diffusion in pondwater acclimated animals, not in a steady state, due to a reduced level of active transport. However, exchange diffusion is substantially reduced following salt depletion and active transport becomes the principal component of J_i^{Cl} (Dietz and Branton, 1979). Chloride transport in *C. fluminea* has not been studied extensively.

Previous studies have indicated that Na and Cl are transported from the dilute bathing medium into the animal against the electrochemical gradient (Dietz and Branton, 1975; 1979; Dietz, 1978, 1979). Pondwater is about 1 mM NaCl and blood is about 10–13 mM Cl and 13–20 mM Na. Since the body fluids are negative 10 mV, both Na and Cl are out of equilibrium. More detailed analyses of intact animals are difficult, including attempts to define the mechanism of ion transport. Never-the-less, whole animal studies delineate the problems faced by the organism and suggest specific areas of interest to be investigated using isolated tissues.

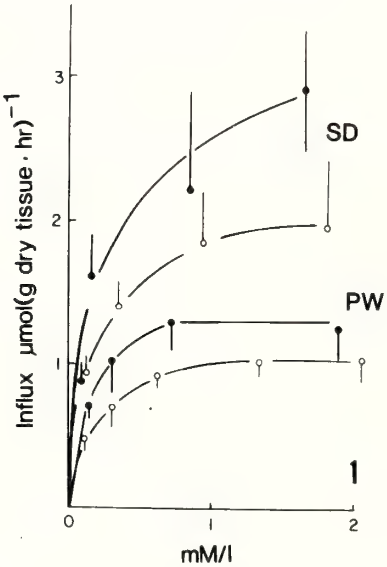

Fig. 1. The effect of Na (•) (Na$_2$SO$_4$) or Cl (o) (choline chloride) concentration in the bath on unidirectional influx in *Carunculina texasensis.* SD refers to salt depleted animals and PW refers to pondwater acclimated mussels. Vertical lines represent ±1 SE (Adapted from Dietz, 1978).

TABLE 1. Unidirectional influxes of Na and Cl partitioned into several components in pondwater (PW) acclimated or salt depleted (SD) mussels. Total influx, J_i^T was calculated from isotope uptake. Exchange diffusion, J_i^{ED}, was calculated from the decrement in efflux when the animals were transferred from dilute salt solution to distilled water. Diffusive flux J_i^D was calculated by the flux ratio equation (see McCorkle and Dietz, 1980). Active transport J_i^{AT} was calculated from $J_i^{AT} = J_i^T - (J_i^{ED} + J_i^D)$.

Species	Condition	Influx μmol (g dry tissue · hr)$^{-1}$			
		J_i^T =	J_i^{ED} +	J_i^D +	J_i^{AT}
Na Influx					
Corbicula	PW	8.8	5.9	0.5	2.4
fluminea[1]	SD	31.4	16.0	1.2	14.2
Ligumia	PW	1.2	< 0.05	<0.03	1.2
subrostrata[2]	SD	2.7	0.1	<0.03	2.5
Cl Influx					
Carunculina	PW	1.0	0.9	<0.02	0.1
texasensis[3]	SD	1.4	0.6	<0.01	0.8

[1] McCorkle and Dietz, 1980. [2] Calculated from Dietz, 1978. [3] Dietz and Branton, 1979.

SITES OF ION TRANSPORT

We have reported that of the several possible sites of Na and Cl uptake (gill, mantle, gut, body surface), the gill is the primary site of Na transport in freshwater mussels (Dietz and Findley, 1980; Dietz and Graves, 1981; Dietz et al., 1982). Isolated gills display saturation kinetics for both Na and Cl transport (Fig. 2). The influx of Na into isolated gills is about 12 μmol Na (g dry gill · 10 min)$^{-1}$ and the transport system has a high affinity (0.17 mM/l) Dietz and Graves, 1981). Since the gills represent about 4% of the total animal weight, then the calculated intact animal influx should be 3 μmol Na (g dry tissue · hr)$^{-1}$. Ordinarily, whole animal influx of Na is 1–2 μmol Na (g dry tissue · hr)$^{-1}$. Not only do the gills account for all the intact animal influx of Na but the results suggest the isolated gill Na transport may be stimulated. Similar studies of Cl transport in isolated gills indicate the gills can account for all Cl uptake by the bivalves (Dietz, unpublished).

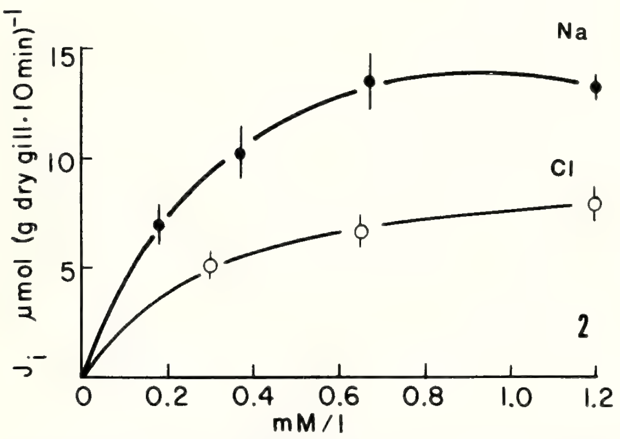

Fig. 2. Effects of Na or Cl concentration in the incubation medium on the unidirectional influx in isolated gills of pondwater acclimated *Ligumia subrostrata*. Vertical lines represent ±1 SE (Adapted from Dietz and Graves, 1981).

ION SENSITIVE ATPases

The characteristics of ion sensitive ATPases have been reported (Table 2) for mussel gill microsomes (Dietz and Findley, 1980) and others have reported on the ATPase characteristics of the mantle and kidney (Saintsing and Towle, 1978; Deaton, 1979; Wheeler and Harrison, 1982). Sodium entering into epithelial cells across the permeable apical membrane is thought to be transported to the blood by a Na/K pump which is driven by Na/K ATPase. The Na/K ATPases are notably low in most of the tissues studied. Of interest is the sensitivity of mussel enzymes to ionic strength of the assay medium. The enzymes in freshwater bivalves appear to be adapted to the dilute intracellular environment. Similarly, Cl transport across epithelial tissue may be driven by the energy supplied by a Cl/HCO_3 or HCO_3 ATPase. Both enzymes are present in gill tissue and display considerable activity. Although an anion exchange model is attractive in its simplicity and has been suggested for vertebrates as well, there is no unanimity of support for the involvement of the anion ATPases in anion transport (see De Renzis and Bornancin, 1977; Schultz, 1978; van Amelsvoort et al., 1978).

CONTROL OF ION TRANSPORT

We have observed diurnal rhythms in Na transport rates in both the unionids and corbiculids (Graves and Dietz,

Table 2. Ion sensitive ATPases in tissues of bivalve molluscs.

		μmol (mg protein · hr)$^{-1}$			
Species	Tissue	Na/K ATPase	Cl/HCO_3 ATPase	HCO_3 ATPase	Mg ATPase
Carunculina texasensis[1]	gill	1.5	0.9	10	12.4
Lampsilis claibornensis[2]	gill	0.8	—	—	11.3
	Mantle	0.5	—	—	6.1
	kidney	7.7	—	—	7.2
Corbicula fluminea[2]	gill	1.2	—	—	35.9
	Mantle	1.9	—	—	42.3
	kidney	0.7	—	—	11.7
Anodonta grandis[3]	mantle	0	—	16	10.7
Rangia cuneata[4]	gill	0.3	—	—	—
	mantle	0.6	—	—	
	kidney	1.0	—	—	—

[1] Dietz and Findley, 1980. [2] Deaton, 1979. [3] Wheeler and Harrison, 1982. [4] Saintsing and Towle, 1978.

1980; McCorkle-Shirley, 1982). In addition, handling some mussel species causes an immediate stimulation of Na influx lasting several hours. These data suggest a fast responding "hormonal" control mechanism regulating Na transport. Moreover, these studies also emphasize the importance of developing an isolated tissue preparation which can be studied independently from the control systems functioning in intact animals.

Some of our studies on intact animals display considerable variability because of the spontaneous changes in endogenous control over ion transport. Both Na and Cl transport are subject to separate regulatory systems. There are several lines of evidence substantiating the presence of control mechanisms for salt balance in mussels. We have reported diurnal changes in ion balance (Graves and Dietz, 1980; McCorkle-Shirley, 1982) and noted the spontaneous stimulation of Na transport in *Margaritifera hembeli* (Dietz, 1979). Salt depletion, by acclimating animals to distilled water, has been used extensively to stimulate ion transport (Krogh, 1939; Murphy and Dietz, 1976; Scheide and Dietz, 1982). Recently, we have documented that selective depletion of either Na or Cl will specifically stimulate the depleted ion transport system. When the animals are returned to the appropriate ionic solution to allow ion repletion, Na or Cl is accumulated by an accelerated ion influx until the normal blood ion concentration is achieved (Scheide and Dietz, 1982).

BIOGENIC AMINE-STIMULATED SODIUM TRANSPORT

Serotonin and catecholamines are potent stimulators of Na transport in mussels (Dietz et al., 1982). We have reported that serotonin and many catecholamines are effective stimulators of Na influx when injected to achieve about 5×10^{-5} M/l blood (Fig. 3) or added to the bath (10^{-4} M/l). When gills are isolated, only serotonin stimulates Na uptake and the catecholamines are ineffective. These data suggest that serotonin stimulates the gill epithelial cells and that serotonergic neurons may be innervated by adrenergic fibers. Substantial concentrations of serotonin are found in the gills of *Ligumia subrostrata* (4 μmol/g gill tissue) and Hiripi (1968) has reported similar amounts in *Unio pictorum*. Since we have reported that injections of cyclic AMP and theophylline stimulate Na transport in mussels (Graves and Dietz, 1982; Dietz et al., 1982), these data suggest a "monoamine" sensitive adenylate cyclase is involved in Na balance (see below).

With the high concentration of serotonin present in the gill tissue we were interested in the localization of serotonin within the gills. Using Procion Yellow, a fluorescent vital stain accumulated by neurons, we identified the general gill innervation pattern. Presumptive serotonergic neurons were identified using formaldehyde-induced fluorescence of biogenic amines (Falck, 1962) (Fig. 4). These two histo-

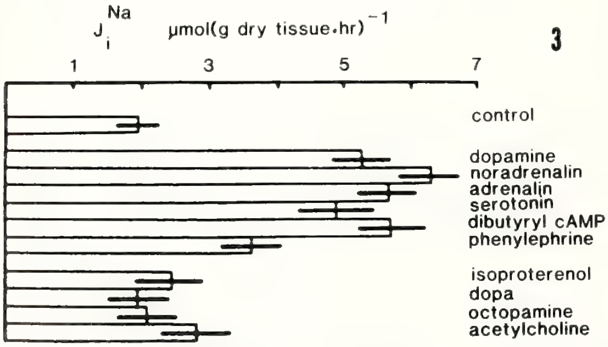

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Fig. 3. The effect of injections of various drugs (~100 nmol/g dry tissue) on the sodium fluxes in pondwater acclimated *L. subrostrata* and *C. texasensis*. There were no differences between species and the data were pooled. Vertical lines represent ±1 SE (Data adapted from Dietz et al., 1982).

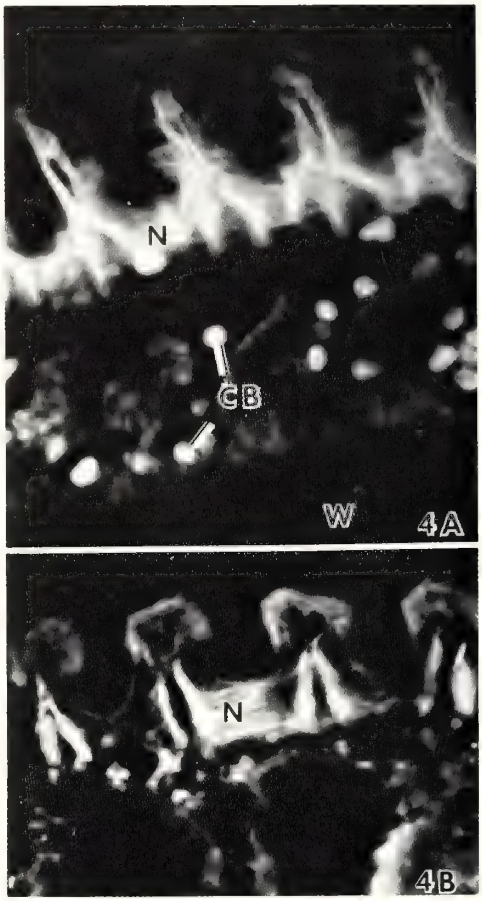

Fig. 4. Fluorescent micrographs of a gill cross-section from *L. subrostrata*. A. Animals injected with Procion Yellow. Fluorescent nerve tracts (N) between gill filaments and cell bodies (CB) are evident in the tissue between the gill filaments and the water channel (W) (field width 450 μm). B. Formaldehyde induced fluorescence having the characteristic yellow color associated with serotonin in nerve tracts (N) between gill filaments. The epithelial cells had a light green autofluorescence (Horizontal field width = 390 μm). (From Dietz et al., 1985).

chemical techniques identified the same discrete nerve tracts in mussel gill tissue (Dietz et al., 1985). We have used transmission electron microscopy to confirm the localization of nerve tract, containing dense vesicles, which branch and innervate the gill epithelia. In addition, we used ^{3}H-serotonin uptake to obtain autoradiographs which displayed high densities of silver grains in the nerve tract regions between the gill filaments and at the base of the water channel epithelium (Fig. 5).

SEROTONIN-STIMULATED ADENYLATE CYCLASE

Since cAMP stimulates Na transport, serotonin may be influencing Na transport via adenylate cyclase-catalyzed cAMP production. Recently, we noted that salt depletion and serotonic treatment increased the cAMP content in isolated gills (Scheide and Dietz, 1983). In addition, we have reported the presence of a serotonin-stimulated adenylate cyclase in gill homogenate (Fig. 6). Addition of micromolar concentrations of serotonin significantly stimulate adenylate cyclase activity (Scheide and Dietz, 1983; 1984). Serotonin stimulates adenylate cyclase (100% or more) above base line rates of cAMP synthesis in gill tissue of several unionids and *C. fluminea* (Fig. 7). The serotonin stimulation of adenylate cyclase can be inhibited selectively by cyproheptadine.

Dopamine also increases adenylate cyclase activity in mussel gills (see Fig. 6) and this catecholamine is effectively inhibited by the antagonist, chlorpromazine (Scheide and Dietz, 1983). Of interest is the observation that dopamine has no effect on Na influx in isolated gills (Dietz et al., 1982). Dopamine may be exerting its effect on gill tissue by increasing the ciliary activity on the epithelial surface (A. Paparo, So. Ill. Univ., pers. comm.). Recently, a number of studies have addressed the biogenic amine stimulation of adenylate cyclase. Adenylate cyclase in the gills of *Aplysia* is stimulated by serotonin (Weiss and Drummond, 1981). Mendelsohn et al., (1981) reported an adrenalin/cAMP stimulation of Cl secretion in fish opercular tissue. Finally, serotonin and dopamine have been observed to stimulate adenylate cyclase in invertebrate nervous tissue (Robertson and Osborne, 1979; Stefano et al., 1981).

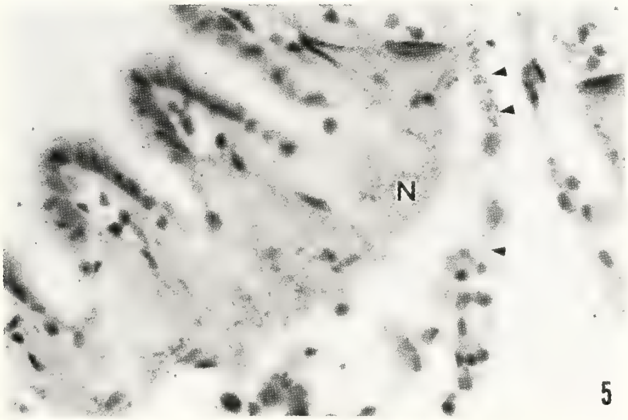

Fig. 5. Bright field autoradiograph of toluidene blue stained gill cross-section from *L. subrostrata* labeled with ^{3}H-serotonin (10^{-12} M). Silver grains are concentrated in the nerve tract (N) region and along nerve fibers at the base of the water channel epithelial cells (arrows) (Horizontal field width = 290 μm). (From Dietz et al., 1985).

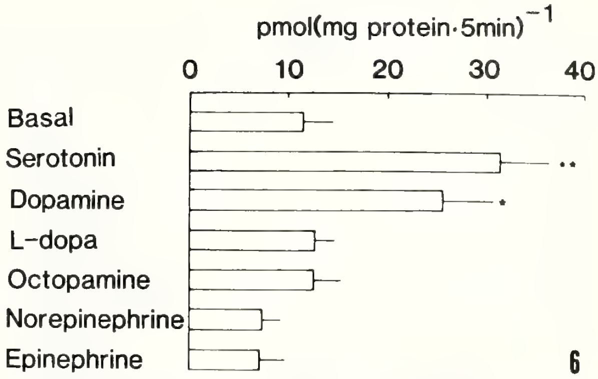

Fig. 6. Adenylate cyclase activity in gill homogenate from *L. subrostrata* exposed to 12 μm of various "monoamines." The horizontal line represents 1 SE. Dopamine (*, $P < 0.05$) and Serotonin (**, $P < 0.01$) are significantly different from basal activity (From Scheide and Dietz, 1983).

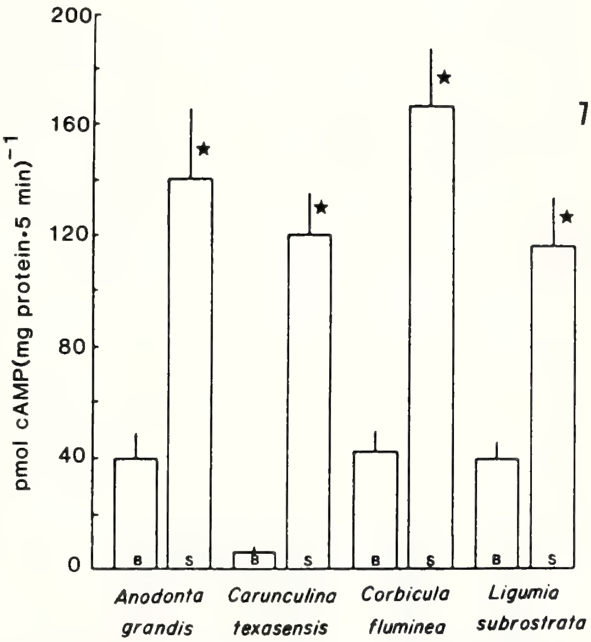

Fig. 7. Basal (B) and serotonin (S) (60 μM/l) stimulated adenylate cyclase activity in the homogenates of gills from 4 species of freshwater mussels. The vertical lines represent 1 SE. * = significantly different from basal activity $P < 0.01$. (From Scheide and Dietz, 1984).

PROSTAGLANDIN INHIBITION OF NA TRANSPORT

Prostaglandins of the diene series (PGE_2 and PGF_{2a}) are synthesized from arachidonic acid by a cyclooxygenase pathway. Prostaglandin E_2 is an effective inhibitor of Na influx in *L. subrostrata* but PGF_{2a} is not (Table 3). We have found that inhibitors of cyclooxygenase (indomethacin, melcofenamate) (Flower and Blackwell, 1976; Flower, 1974) block prostaglandin production in mussels and cause a stimulation in Na transport (Graves and Dietz, 1979; 1982; Saintsing and Dietz, 1983; Saintsing et al., 1983) (Table 3). Prostaglandins are widely distributed in animals and have been extensively implicated in modulating ion transport in gills, toad bladder and kidney (Nomura and Ogata, 1976; Zusman et al., 1978; Orloff and Zusman, 1978; Freas and Grollman, 1980, 1981; Korff and Jarabok, 1980; Zusman and Keiser, 1980).

We have developed radioimmuno-assay techniques for measuring prostaglandins in mussel blood using specific antibodies (Saintsing, et al., 1983) and Freas and Grollman (1980) have measured prostaglandins in the gills of *Modiolus demissus*. Both PGE_2 and PGF_{2a} are present and preliminary data suggest prostacyclin is synthesized but thromboxane is not detectable in mussel blood. Arachidonic acid is a major fatty acid in the mussel gill phospholipids as measured by gas chromatography (Pollero et al., 1981a, b; Saintsing et al., 1983; A. Hagar and T. Dietz, unpublished). We have initiated studies of the prostaglandins synthesized by the cyclooxygenase pathway in mussel gill tissue (Saintsing et al., 1983; A. Hagar and T. Dietz, unpublished). In addition, we have noted lipoxygenase metabolites of arachidonic acid are produced by gill homogenate. However, we do not know what role the hydroperoxyeicosatetraenoic acids (HPETE's, leukotrienes?) play in the physiology of bivalves (Fig. 8).

ROLE OF CALCIUM CONCRETIONS IN BIVALVE GILLS

Recently, we have observed a substantial amount of calcium concretions in the gill tissue of mussels (Silverman et al., 1983; 1985; Steffens et al., 1985) (Fig. 9). Since gill tissue is not a direct component of the shell forming tissue, it is probable that the concretions are serving as a Ca reservoir. We have documented that Ca concretions increase in mass under hypoxic conditions (Silverman et al., 1983). Our hypothesis is that the concretions in the gill are serving as a Ca source possibly for osmoregulation by cation exchange and as a Ca source for shell formation of larvae in reproductively active females (see below). Morphologic studies of unionid gills have demonstrated an extensive neuronal network in parallel association with calcium concretions (Dietz et al., 1985; Silverman et al., 1983; 1985; Steffens et al., 1985). Similar appearing concretions have been reported in other mollusc tissues and in the mantle tissue where they may play a role in shell formation (Abolins-Krogis, 1970; Petit et al., 1980; Davis et al., 1982).

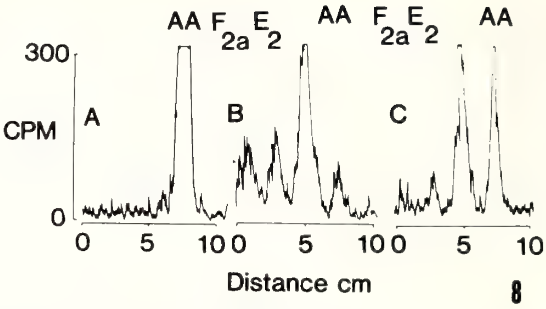

Fig. 8. Metabolism of ^{3}H-arachidonic acid (AA) by gill homogenate from pondwater acclimated *L. subrostrata*. A. ^{2}H-arachidonic acid incubated 60 min with boiled homogenate. B. ^{3}H-arachidonic acid incubated with homogenate. C. ^{3}H-arachidonic acid incubated with homogenate in the presence of 1 mM meclofenamate. Prostaglandin E_2 and F_{2a} standards are indicated at the top of the chromatograms (From Saintsing et al., 1983).

We have qualitatively identified Ca in the concretions histochemically on sectioned frozen gill tissue. In addition, we have separated the concretions in pure form (as determined by electron microscopy) by homogenizing the tissue and either digesting the tissue with 1 N NaOH at 60° C for 1 hr (concretion appearance is not affected) or layering the

Table 3. Effects of injections of prostaglandin (PG) biosynthesis inhibitors, 5HT and cAMP on blood PG concentrations and J_n^{Na} in pondwater acclimated *Ligumia subrostrata* (from Saintsing et al., 1983).

Treatment	N	Dose μmol/g dry tissue	PGE_2 ng/ml	J_n^{Na} μmol (g dry tissue · hr)$^{-1}$
Control	50	—	0.39	−0.02
Meclofenamate	9	0.81	0.18**	1.76**
Indomethacin	10	0.28	0.09**	2.41**
Serotonin	10	0.12	0.14**	1.85**
cAMP	10	1.88	0.21*	2.57**

Significantly different from corresponding controls, $^*P < 0.05$; $^{**}P < 0.01$.

Fig. 9. Light micrograph of toluidene blue stained freeze-dried *Anodonta grandis* gill. The cross-section demonstrates the dense accumulation of concretions (C) below the gill filaments (F) (From Silverman et al., 1985) (Horizontal field width = 3.7 mm).

homogenate over 2.5 M sucrose and centrifuging the concretions into the discontinuous gradient. The purified concretions amount to 25–50% of the gill weight and by extracting the concretions in acid we have found 20–30% of the mass was Ca (determined by atomic absorption) (Table 4). The chemical analyses were confirmed by energy dispersive X-ray spectroscopy where Ca and P were the principal elements and Fe and Mn were found to be minor components (Fig. 10) (Steffens, unpublished).

The concretions in *Ligumia subrostrata* contain 25% volatile (at 450° C) organic material. The nature of this material is unknown, but it does not contain appreciable amounts of either oxalate (M. Hatch, La. State Univ., unpublished) or carbonate. By histochemical analyses, glycoprotein appears to be present. Recently, we prepared polyclonal antisera against the concretion organic material (Steffens et al., 1985). Antisera against concretions from one unionid species cross-react with all other species of unionids examined; indicating the conservative nature of at least one organic component. Such conservation may indicate an important function for these concretions and their calcium binding ability.

Most studies of ion regulation in aquatic animals have focused on Na and Cl and their potential exchange ions NH_4, H, or HCO_3. However, in our previous studies, we noted the importance of Ca in osmo-regulation in freshwater mussels.

Table 4. Chemical composition of concretions isolated from pondwater acclimated *L. subrostrata* (from Silverman et al., 1983).

Concretion content	(g/g dry gill)	0.25
Ash (450° C)	(g/g dry concretion)	0.75
Volatile organic	(g/g dry concretion)	0.25
Calcium	(g/g dry concretion)	0.25
Phosphorous	(g/g dry concretion)	0.13
(calculated as PO_4 or P_2O_7)		0.37–0.40
HCO_3	(g/g dry concretion)	0.03
Unidentified	(g/g dry concretion)	0.07

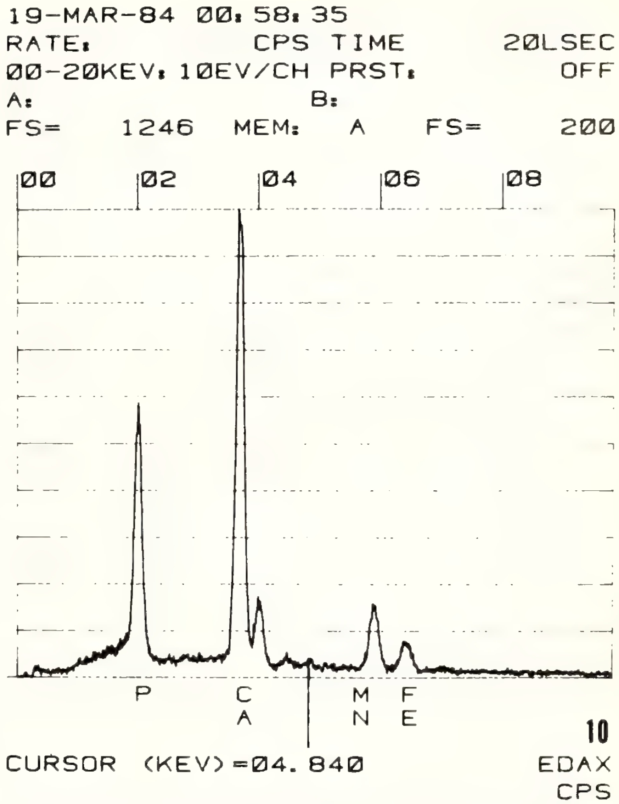

Fig. 10. Energy dispersive X-ray spectrum of purified concretions from the gill of *L. subrostrata*. Calcium and phosphorous are the major components with manganese and iron being minor constituents (Steffens, unpublished).

There is an inverse relationship between blood Na and Ca. When the animals are salt depleted in de-ionized water, selectively depleted of Na by acclimation to choline chloride or subjected to anoxia, the blood Na declines from 15–20 mM to < 10 mM while Ca increases from 3–5 mM to 8–20 mM (Dietz, 1974; Murphy and Dietz, 1976; Scheide and Dietz, 1982; Silverman et al., 1983). Recently, we determined the net flux of Ca while measuring the net flux of Na and noted a direct relationship between the loss of Ca and the gain of Na (Scheide and Dietz, unpublished). The relationship between Na/Ca exchange is $J_n^{Ca} = -0.5 J_n^{Na} - 1.51$ ($r - 0.55$; $P < 0.001$). The relationship pertained to pondwater acclimated controls, salt depleted or serotonin treated animals. The source of Ca for the Na/Ca exchange is unknown but the concretions in the gill would be in a suitable location for Na/Ca exchanged in both intact animals and isolated gills.

Recently, we have observed the disappearance of calcium concretions when the animals enter the reproductive period (Silverman, et al., 1985). Calcium concretions are X-ray dense in relation to other soft body parts and a loss of density coincides with the mobilization of the concretions during the early reproductive period in female *Ligumia subrostrata* (not shown) and *Anodonta grandis* (Fig. 11). Possi-

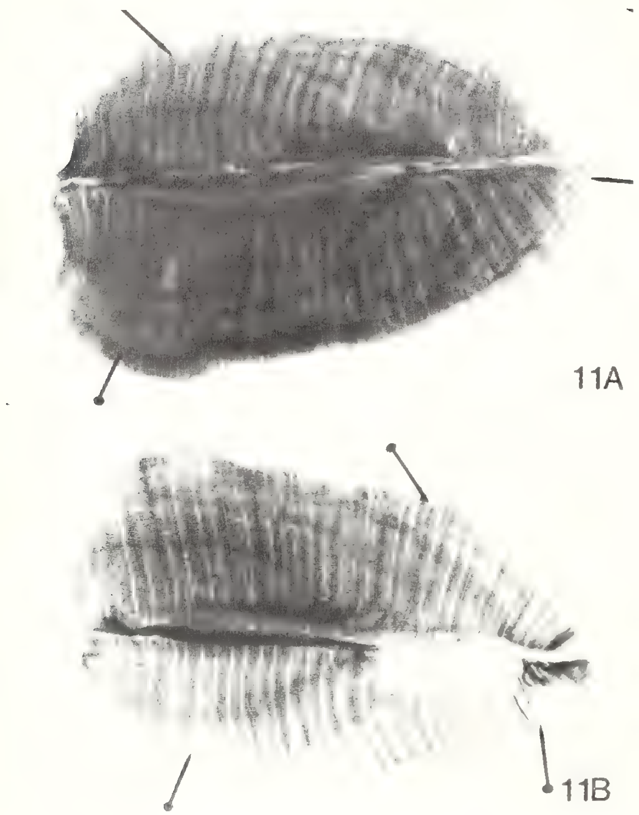

Fig. 11. X-ray radiograms of a pair of gills from *A. grandis* before and during reproductive activity. Both A and B were exposed to the same X-ray parameters and photographic development conditions. A. A gill from an animal before reproduction. The parallel lines of dense concretion material extend nearly to the leading edge of the gill. B. A gill from an animal containing early larval glochidial stages with calcified valves. The concretions have been mobilized mostly from the lateral marsupial gill but loss of concretions is evident from the medial gill. A small rectangle of one surface of the gill was removed to demonstrate that the concretions were present on both lamellae (From Silverman et al., 1985) (Horizontal field width = 8.3 cm).

bly the liberated calcium is available for shell growth in these animals. However, the calcium is mobilized in the female gills after the fertilized eggs begin developing in the gill marsupium and may provide a source of Ca for the embryonic shell formation. We have observed that *A. grandis* broods substantially more embryos in the gills and has twice the calcium concretions when compared to *L. subrostrata*. In addition, preliminary evidence indicates radioactivity appears in the glochidial shells when concretions labelled with ^{45}Ca are mobilized by the females. Further studies are required to understand the mechanism of Ca transfer and the role of Ca in Na balance. Calcium may be important in the transepithelial Na transport process in bivalves, and may be particularly important when the animal is under stress: reproductive, anoxic and/or osmotic.

ACKNOWLEDGEMENTS

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SEASONAL RESPIRATORY VARIATION AND METABOLIC COMPENSATION FOR TEMPERATURE AND HYPOXIA IN THE FRESHWATER SNAIL, *PHYSELLA VIRGATA VIRGATA* (GOULD), WITH SPECIAL REFERENCE TO THE EFFECTS OF HEATED EFFLUENTS[1]

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ABSTRACT

Specimens of the freshwater, basommatophoran snail, *Physella virgata virgata*, were collected monthly from September to April over 1973–1974 and 1974–1975, and during the summer of 1976 from two populations in Lake Arlington, Tarrant Co., North Central Texas. One population was isolated on a rocky shore receiving heated effluents from a steam-electric power station. A second population was isolated on the rocky shore of the lake's main dam where annual ambient water temperature averaged 5°C less than in discharge areas. At each collection the oxygen consumption rates ($\mathring{V}_{O_2}$) of selected individuals were monitored in response to progressive hypoxia at 25°C and to acute temperature change from 5°C to the upper thermal limit (45°C or 50°C). *P. virgata virgata* was a moderate regulator of $\mathring{V}_{O_2}$ (Critical $Po_2 \approx 70$ torr; mean $B^2 \times 10^3 \approx -0.0607$ to -0.0619). No interpopulation or seasonal variation in regulatory ability was detected. $\mathring{V}_{O_2}$ increased with increasing temperature up to 35°C or 40°C. The temperature of maximum $\mathring{V}_{O_2}$ increased with increasing ambient water acclimatization temperature. Over 5°C to 40°C, respiratory Q_{10} values increased with increasing ambient water acclimatization temperature, indicating an apparent seasonal temperature compensation of metabolic rate. In both populations metabolic temperature compensation involved counter clockwise rotation of $\mathring{V}_{O_2}$-temperature (R-T) curves about a pivot point of 30°C with acclimatization to increasing ambient water temperature, whereby warm-conditioned individuals displayed a lower $\mathring{V}_{O_2}$ than cold-conditioned individuals below 30°C, but a greater $\mathring{V}_{O_2}$ above that temperature. Such seasonal rotation of the R-T curve produces a pattern of partial metabolic temperature compensation that may function to allow maintenance of activity at levels which sustain a positive bioenergetic balance in overwintering individuals. However, above 30°C a seasonal pattern of "reverse" or "inverse" metabolic compensation occurs. Natural populations of *P. virgata virgata* rarely experience field temperatures above 30°C. However, ambient water temperatures above 35°C were common in the heated discharge area. Under these conditions the counter clockwise rotation of the R-T curve about 30°C in warm (summer)-conditioned individuals may induce an energetically non-adaptive elevation of metabolic rate. There were no significant differences ($P > 0.05$) between the respiratory responses of the two populations to hypoxia, acute temperature change, or seasonal temperature variation, indicating that exposure to thermal effluents had not caused the selection of a metabolically adapted race.

There have been a number of studies of metabolic temperature compensation in freshwater pulmonate (for a review see McMahon, 1983) and prosobranch snails (for a review see Aldridge, 1983). Of these, only a relatively few have involved repeated determinations of oxygen consumption rates in field acclimatized individuals in conjunction with concurrent studies of life cycle, reproduction, and condition, and all of these have been limited to ancylid limpets, the most advanced and aquatic of all freshwater basommatophoran species (for a review see McMahon, 1983). All the ancylid species studied, *Ancylus fluviatilis* (Müller) (Berg, 1952; Berg, et al., 1958), *Ferrissia rivularis* (Say) (Burky, 1971), and *Laevapex fuscus* (C. B. Adams) (McMahon, 1973) display an unusual pattern of respiratory compensation for seasonal temperature fluctuation referred to as "reverse" or "in-

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verse" acclimation (Precht, 1958; Prosser, 1973), whereby warm-acclimated specimens have higher oxygen consumption rates than cold-acclimated individuals at any one test temperature.

Laboratory studies of more primitive lymnaeid, physid and planorbid pulmonate species, which retain the pulmonary cavity for aerial gas exchange and a diving habit (McMahon, 1983), indicate that they display the more typical pattern of partial metabolic compensation for long-term temperature variation whereby the oxygen consumption rate of warm-acclimated individuals is less than that of cold-acclimated individuals at any one test temperature (Berg and Ockelmann, 1959; Beames and Lindeborg, 1967; Daniels and Armitage, 1969; Prosser, 1973; Calow, 1975; Wood, 1978; Meakins, 1980). However as none of these investigations involved detailed concurrent studies of seasonal variation in the metabolic rates of field-conditioned individuals, or of a species' population biology and ecology, it is difficult to attribute an adaptational significance to the patterns of metabolic temperature compensation observed in the laboratory. Indeed, even the hypothesis that metabolic compensation confers some degree of metabolic independence from seasonal temperature variation in ectothermic animals has been recently criticized (Parry, 1984). In the vast majority of cases, the adaptive value of a species' pattern of metabolic compensation can only be elucidated when accompanied by studies of its population dynamics and ecology.

In addition, little is known of seasonal effects on the metabolic response to hypoxia of freshwater pulmonate snails. Many freshwater pulmonate species have been observed to migrate to deeper waters (lymnaeids and physids) or to burrow into the substratum to overwinter (planorbids and some ancylids) (McMahon, 1983), where reduced environmental oxygen concentrations may be encountered. The only published study of seasonal variation in the metabolic response to hypoxia of a freshwater gastropod (McMahon, 1973) has indicated that declining ambient water temperatures induce a shift towards increased regulation of oxygen consumption as an apparent adaptation to a hypoxic overwintering environment.

This paper presents an evaluation of the adaptational significance of seasonal variation in the metabolic response to temperature and hypoxia in two populations of a more primitive, diving species of freshwater pulmonate snail, *Physella virgata virgata* (Gould, 1855), which retains the pulmonary cavity as an organ of aerial gas exchange. The first of these populations was restricted to a rocky substratum in an area of a lake receiving thermal effluents for 18 years, or 54 generations (McMahon, 1975a, 1976a) and had a higher thermal tolerance than a second population collected on the rocky shore of the main dam of the same lake where water temperatures averaged 5°C less than that to which the discharge population was exposed. A concurrent study detailed the growth, reproduction and life histories of these two populations (McMahon, 1975a) and formed the basis on which hypotheses regarding the adaptive value of this species' seasonal metabolic compensation were formulated. Also examined was the hypothesis that the selection pressures associated with exposure to thermal effluents may have induced the development of specific metabolic temperature adaptations in the discharge population.

MATERIALS AND METHODS

SPECIES AND COLLECTING SITES

The ubiquitous freshwater pulmonate snail, *Physella virgata virgata,* is found from Nebraska west to California, and east to Texas, extending south into Mexico (Burch, 1982). This species is very common in North Central Texas where it is equally successful in lentic and lotic habitats (McMahon, 1975a). While highly euryoecic, it is restricted to shallow, near-shore waters and hard substrata such as rocks, wood, leaves, emergent macrophytic vegetation or other hard surfaced debris (McMahon, 1975a).

Specimens of *P. virgata virgata* were collected monthly from September to April over both 1973–1974, and 1974–1975, and from June through August in 1976, from two sites on Lake Arlington, Tarrant County, Texas. Lake Arlington (Fig. 1), formed from the artificial impoundment of Village Creek in 1957, has a total surface area of 920.7 ha and a total capacity of 56 × 10^6 m^3 (Dowell and Breeding, 1966). The natural substratum of the lake was a mixture of fine sand and mud, avoided by *P. virgata virgata.* Therefore, *P. virgata virgata* populations were reproductively isolated in two areas of the lake with artificial rocky shores. The first of these was the shore of the main dam of the lake, covered with chalky lime stone boulders to prevent erosion. Snails were collected from a site hereafter referred to as LAD (Lake Arlington Dam) on the eastern edge of the dam near the outlet of Village Creek (Fig. 1). The second collection area was another artificial rocky erosion barrier on the western shore of an island facing into a cooling pond (Hot Pond) receiving thermal effuents from the Handley Steam-electric Power Station, then operated by the Texas Electric Service Company. This site is hereafter designated as LAOL (Lake Arlington Outlet) (Fig. 1). The Hot Pond was formed by connecting the island to the shore proper by a dam diverting thermal effluents from the steam condensers of the plant's three generating units into an inlet area behind the island (Fig. 1). Maximum discharge rate was 1.87 × 10^9 l/day, and the monthly average rate was 1.514 × 10^9 l/day (McMahon, 1975a). Ambient water temperatures at LAOL were 2° to 10° C higher than those recorded at LAD, unaffected by heated effluents (McMahon, 1975a, 1976a; and Fig. 2).

Snails were collected at both sites by removing all attached individuals with a scalpel blade from rocks lifted from the substratum. Snails were returned to the laboratory within two hours of collection and maintained at field ambient temperature (±0.5°C) in an incubator in 1.0 l wide-mouth jars filled with lake water from the collection site. Conductivity, pH, and ambient air and water temperatures were recorded at each collection.

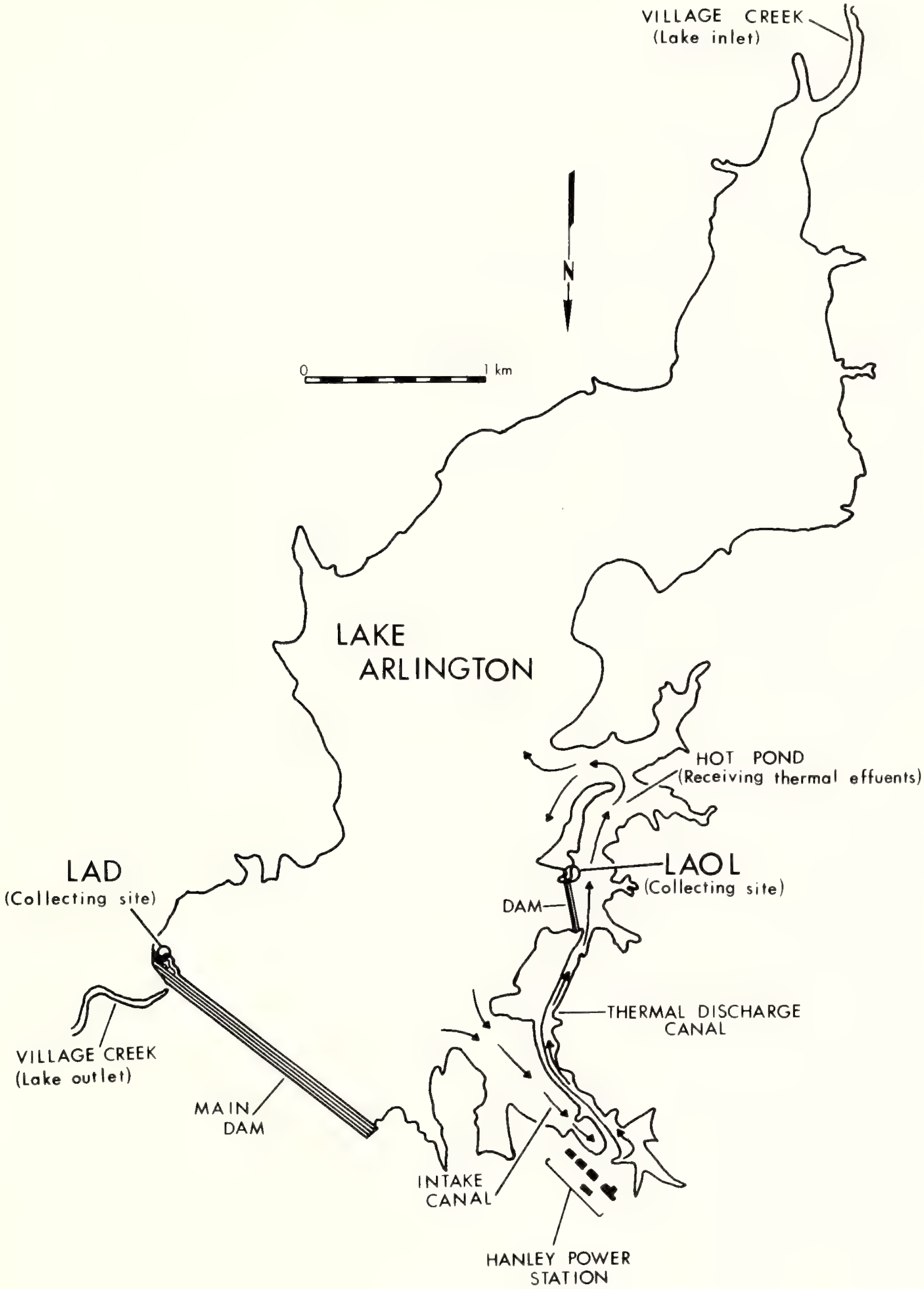
VILLAGE CREEK
(Lake inlet)
N
0
1 km
LAKE
ARLINGTON
HOT POND
(Receiving thermal effuents)
LAD
(Collecting site)
LAOL
(Collecting site)
DAM
THERMAL DISCHARGE
CANAL
VILLAGE CREEK
(Lake outlet)
MAIN
DAM
INTAKE
CANAL
HANLEY POWER
STATION

Fig. 1. Map of Lake Arlington in Tarrant County, Texas, showing collection sites for *Physella virgata virgata*. LAD is the collection site of a population isolated on a limestone boulder shore on the main dam of the lake. LAOL is the collection site for a second population isolated on a limestone boulder shore in an inlet (Hot Pond) of the lake receiving thermal effluents from the Handley Steam-electric Power Station. Arrows indicate flow of raw lake water through intake canal into generator turbine steam condensers of power station and, as heated effluents, from power station's steam condensers down thermal discharge canal into Hot Pond from which it returns to the lake.

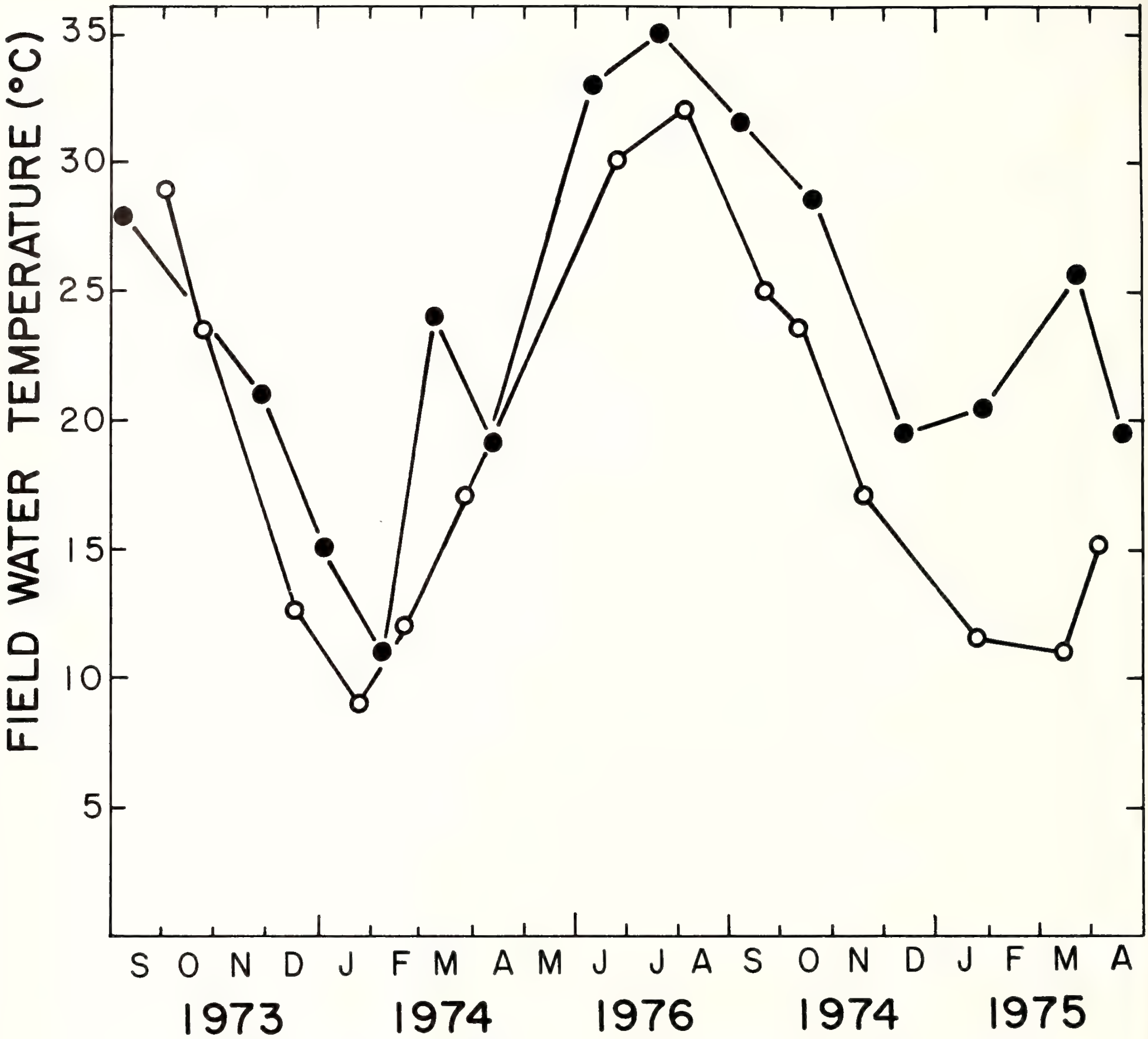

Fig. 2. Field ambient water temperatures at the two *Physella virgata virgata* collecting sites on Lake Arlington, Texas. Ambient water temperature in °C (vertical axis) at each collection is represented over duration of collection periods (horizontal axis) by open circles for LAD collection site and by solid circles for LAOL collection site which receives thermal effluents. Note that summer records of ambient water temperature taken from June through August of 1976 are plotted between September and May sampling periods of 1973–1974 and 1974–1975, to indicate annual pattern of ambient water temperature variation at each site.

DETERMINATION OF OXYGEN CONSUMPTION RATES

Determinations of routine oxygen uptake rates ($\mathring{V}o_2$) took place within 48 h of collection. $\mathring{V}o_2$ was monitored with YSI model 53 silver-platinum, polarographic oxygen electrodes, modified by insertion of a glass annulus at the base of the respiration chamber to support a magnetic stirrer above the snails (Burky, 1977). Stirring chamber water did not affect the behavior of experimental individuals which locomoted freely over the chamber floor and walls during $\mathring{V}o_2$ determinations. Chamber water volume for all determinations was 4 ml. Chamber water was filtered, sterilized lake water taken from the collection site. Bacterial growth during $\mathring{V}o_2$ determinations was inhibited by addition of streptomycin to chamber water, which did not affect snail behavior or electrode performance. Chamber water temperature was controlled within ± 0.05°C of experimental temperature with a Lauda K-2/R constant temperature circulator. Prior to $\mathring{V}o_2$ determinations the shell lengths (SL; the longest anterior-posterior dimension from the tip of the spire to the leading edge of the aperture) of experimental individuals were measured to the nearest 0.1 mm on a stage micrometer at 10x power under a dissecting microscope. Experimental individuals were then separated into subsamples (number in subsample depending on shell length) in which all individuals had an SL within ± 2.5 mm of a chosen median value.

METABOLIC RESPONSE TO TEMPERATURE

In one set of experiments the $\mathring{V}o_2$ of six different subsamples from each collection (SL range of subsamples chosen to be modally representative of the range of SL in the natural population) was monitored over a temperature span extending from 5°C to 45°C or 50°C (which surpassed the upper lethal temperature) in 5°C intervals. Before being placed in the respiration chamber, the foot of each snail was touched lightly with a fine tipped paint brush to cause withdrawal into the shell, expelling the air in the pulmonary cavity. Specimens were placed in the chambers at field ambient water temperature. Thereafter, water temperature was lowered at a rate of 1.0°C/5 min until a temperature of 5°C was reached. After equilibration of the O_2 electrode for 30 min in a blank chamber containing only sterilized lake water, it was inserted into an experimental chamber (with snails) held at near full air saturation with 0_2 ($Po_2 \approx 159$ Torr) by constant stirring and exposure to the atmosphere. The 0_2 consumption of the subsample of snails was then monitored over the first 10% reduction of Po_2, or for one hour if less than 10% of the available 0_2 was utilized during that period. Thereafter, chamber water temperature was raised from 5°C to 10°C and after equilibration of the electrode in the blank chamber for 30 min, the $\mathring{V}o_2$ of each subsample was determined as described above. This procedure was repeated at 5°C intervals until the upper lethal temperature was surpassed at 45°C or 50°C.

METABOLIC RESPONSE TO HYPOXIA

In a second set of experiments the metabolic response to progressive hypoxia at 25°C was recorded for three subsamples of adult snails (subsample modal $SL > 4.0$ mm) from collections taken from October through April in 1974–1975, and from June through August in 1976. Determination of $\mathring{V}o_2$ was as described above for respiratory response to temperature except that monitoring of 0_2 consumption rates continued throughout the entire range of 0_2 concentration from full air saturation ($Po_2 \approx 159$ torr) to that at which significant 0_2 uptake ceased ($Po_2 < 8$ torr).

For each subsample $\mathring{V}o_2$ was computed for each 10% decrease in Po_2 until 30% of air saturation levels were reached. Thereafter, $\mathring{V}o_2$ was computed for every 5% decline in Po_2 until all significant 0_2 consumption ceased. Preliminary experiments indicated that temperature did not significantly affect the metabolic response of *P. virgata virgata* to hypoxia, therefore, all experiments were carried out at 25°C, chosen to be representative of the annual average ambient water temperature at the two collecting sites (Fig. 2).

DETERMINATION OF TISSUE AND SHELL DRY WEIGHTS

After completion of all $\mathring{V}o_2$ determinations, individuals in each subsample were dried at 95°C and the constant dry weight recorded to the nearest 0.1 mg. Thereafter, the mineral components of the shell of dried specimens was dissolved in 12% nitric acid by volume (McMahon, 1973, 1975a). The shell periostracum and organic matrix were then removed and the remaining body tissue rinsed three times in tap water. Body tissues were then redried at 95°C to constant dry weight (± 0.05 mg). The dry shell weight (DSW) was then estimated by subtracting the dry tissue weight (DTW) from the total dry weight (TDW).

RESULTS

PHYSICAL PARAMETERS OF LAKE ARLINGTON WATER

During the course of the study pH ranged from 7.3 to 8.85 at LAD (mean pH computed from mean H^+ concentration = 8.8, 95% confidence limit = 7.78 −8.6, n = 19) and from 6.8 to 8.9 at LAOL (mean pH = 7.66, 95% confidence limit = 7.36 − 9.4, n = 18). Conductivity ranged from 190 μmho cm^{-2} to 390 μmho cm^{-2} at LAD (mean = 294 μmho cm^{-2}, s.d. = ± 69, n = 20), while conductivity ranged from 190 μmho cm^{-2} to 389 μmho cm^{-2} at LAOL (mean conductivity = 288 μmho cm^{-2}, s.d. = ± 70, n = 19). Ambient air temperature at LAD ranged from 8°C to 33°C (mean ambient air temperature = 20.2°C, s.d. = ± 6.9°C, n = 21) and from 8.5°C to 31°C at LAOL (mean ambient air temperature = 20.6°C, s.d. = ± 7.2°C, n = 19). Ambient water temperatures at LAD ranged from 9°C to 32°C (mean ambient water temperature = 19.3°C, s.d. = ± 6.8, n = 21) while water temperatures at the LAOL site receiving thermal effluents were higher, ranging between 11.0°C and 35.5°C (mean ambient water temperature = 24.2°C, s.d. = ± 6.7, n = 19) (Fig. 2).

Mean pH, conductivity, and ambient air temperature were all insignificantly different between the two sites ($P > 0.2$). In contrast, mean water temperature was significantly higher at LAOL, which received thermal effluents ($t = 2.30$, $P < 0.05$, df = 38), indicating that water temperature was the only major physical water parameter significantly affected by passage through turbine steam condensers. Maximum differences in ambient water temperature between the two sites occurred in January and February, 1975, when water temperatures at the thermally influenced LAOL collecting site were 10–15°C higher than those recorded at the LAD site (Fig. 2).

STANDARD INDIVIDUALS FOR $\dot{V}o_2$ ESTIMATIONS

The grand mean SL for combined subsamples from LAD and LAOL utilized in $\dot{V}o_2$ determinations was 6.1 mm (s.d. ± 2.4, s.e. = ± 0.2, n = 168). Similarly, the grand mean individual dry tissue weight (DTW) for all subsamples was 2.2 mg (s.d. = ± 2.7, s.e. = ± 0.2, n = 168). When subsample mean DTW was converted to common logarithmic values and fitted to a least squares linear regression versus mean SL (Zar, 1974) the following regression resulted:

$$\text{Log}_{10}\ \text{DTW in mg} = -1.026 + 0.186\ (\text{SL in mm});$$
$$(r = 0.882,\ F = 1241,\ n = 168,\ P < 0.0001).$$

To determine the standard individuals on which all comparative estimations of $\dot{V}o_2$ would be based, the SL of an individual with a DTW equal to the grand mean DTW of all the subsamples (grand mean DTW = 2.2 mg) was estimated from the above regression equation to be 7.5 mm (rounded to the nearest 0.5 mm) with a DTW of 2.34 mg. From this value the SL of two other standard individuals was computed by adding or subtracting the standard deviation of the grand mean of the subsample means rounded to the nearest whole number (s.d = ± 2.0) to the standard 7.5 mm SL individual giving standard individuals with an SL of 5.5 mm and 9.5 mm, respectively. The regression equation relating the $\log_{10}$ of mg DTW to mm SL described above was then utilized to estimate the DTW of each of these two standard individuals as 0.94 mg and 5.51 mg, respectively. Utilization of standard individuals with a constant DTW to estimate $\dot{V}o_2$ eliminates variation in $\dot{V}o_2$ resulting from seasonal changes in the DTW of individuals of constant SL (see below) and allows direct comparisons of $\dot{V}o_2$ across time.

DRY TISSUE WEIGHT : DRY SHELL WEIGHT RATIOS

For each collection period the mean DSW (mg) and mean DTW (mg) of each subsample utilized in $\dot{V}o_2$ determinations were transformed into common logarithms and fitted to separate least squares linear regressions versus SL in mm (n = 6–9 for each collection). The DTW and DSW of three individuals with standard shell lengths of 5.5 mm, 7.5 mm and 9.5 mm (chosen as described above) were then estimated from the appropriate regression. These values were then converted to DTW:DSW ratios. The DTW:DSW ratio is a measure of condition with increased DTW:DSW ratios indicating an increase in tissue mass relative to that of the shell which is assumed to remain constant in a particular size class. High DTW:DSW ratios are, therefore, associated with growing individuals in good condition (Williams and McMahon, 1985).

The pattern of annual variation in this ratio is similar in both the LAD and LAOL *P. virgata virgata* populations. The DTW:DSW ratio remained low throughout late fall and winter and increases in the spring, reaching peak values in March just prior to the onset of ovipostion (for details of the reproductive cycle in these populations see McMahon, 1975a). In the LAD population this ratio declines to winter levels throughout the oviposition period from April through July, while in the LAOL population the DTW:DSW ratio did not begin to decline until after June well after oviposition had been initiated (Figs. 3A–C).

METABOLIC RESPONSE TO HYPOXIA

For each subsample of *P. virgata virgata* for which $\dot{V}o_2$ was monitored during progressive hypoxia, $\dot{V}o_2$ values computed at each sequential 0_2 concentration (expressed as $\mu l\ 0_2\ (\text{STP}) \cdot \text{animal}^{-1} \cdot \text{hr}^{-1}$) were standardized by expressing them as fractions of the rate at full air saturation with 0_2 ($Po_2 \approx 159$ torr). These standardized $\dot{V}o_2$ values were then fitted versus Po_2 in torr as the X value to a quadratic equation (Zar, 1974). The resultant quadratic coefficient (b_2) is a predictor of the degree of regulation of oxygen consumption rate with progressive hypoxia. Expressed as $b_2 \times 10^3$ it becomes an increasingly negative value as the degree of regulation increases (Mangum and Van Winkle, 1973). Values of $b_2 \times 10^3$ greater than -0.02 are generally indicative of a non-regulator of $\dot{V}o_2$, while those less than -0.085 are indicative of nearly perfect regulation of $\dot{V}o_2$ (for details of the application of the quadratic coefficient to the analysis respiratory response to hypoxia see Mangum and Van Winkle, 1973; for a review of its application in freshwater pulmonates see McMahon, 1983). This sort of analysis indicated that the majority of individuals of *P. virgata virgata* were generally moderate to good regulators of $\dot{V}o_2$ ($b_2 \times 10^3 = -0.069$ to -0.020) (Table 1). However, some individuals displayed relatively poor regulatory ability ($b_2 \times 10^3 > -0.02$).

Least squares linear regression analysis indicated that there was no significant relationship (n = 18–19, r = 0.084–0.146, F = 0.123–0.35, P > 0.5) between regulatory ability and size expressed as DTW at either site. Nor was there any discernable pattern of seasonal variation in regulatory ability as least squares linear regression analysis did not reveal a significant relationship between subsample $b_2 \times 10^3$ values and ambient water temperature (n = 18–19, r = −0.028–0.215, F = 0.012–0.777, P > 0.5).

As there were no significant seasonal, size, or temperature effects on the regulatory ability of *P. virgata virgata* at 25°C a mean of the standardized $\dot{V}o_2$ values for all subsamples at each site was then computed for each successive level of hypoxia over the full range of 0_2 tensions tested (Po_2 range $\approx 159 - < 8$ torr) (Fig. 4). T-tests comparing the mean standardized $\dot{V}o_2$ values for LAD and LAOL experimental subsamples at specific 0_2 tensions indicated that there were no significant differences in these values between the two populations over the entire range of Po_2 for which

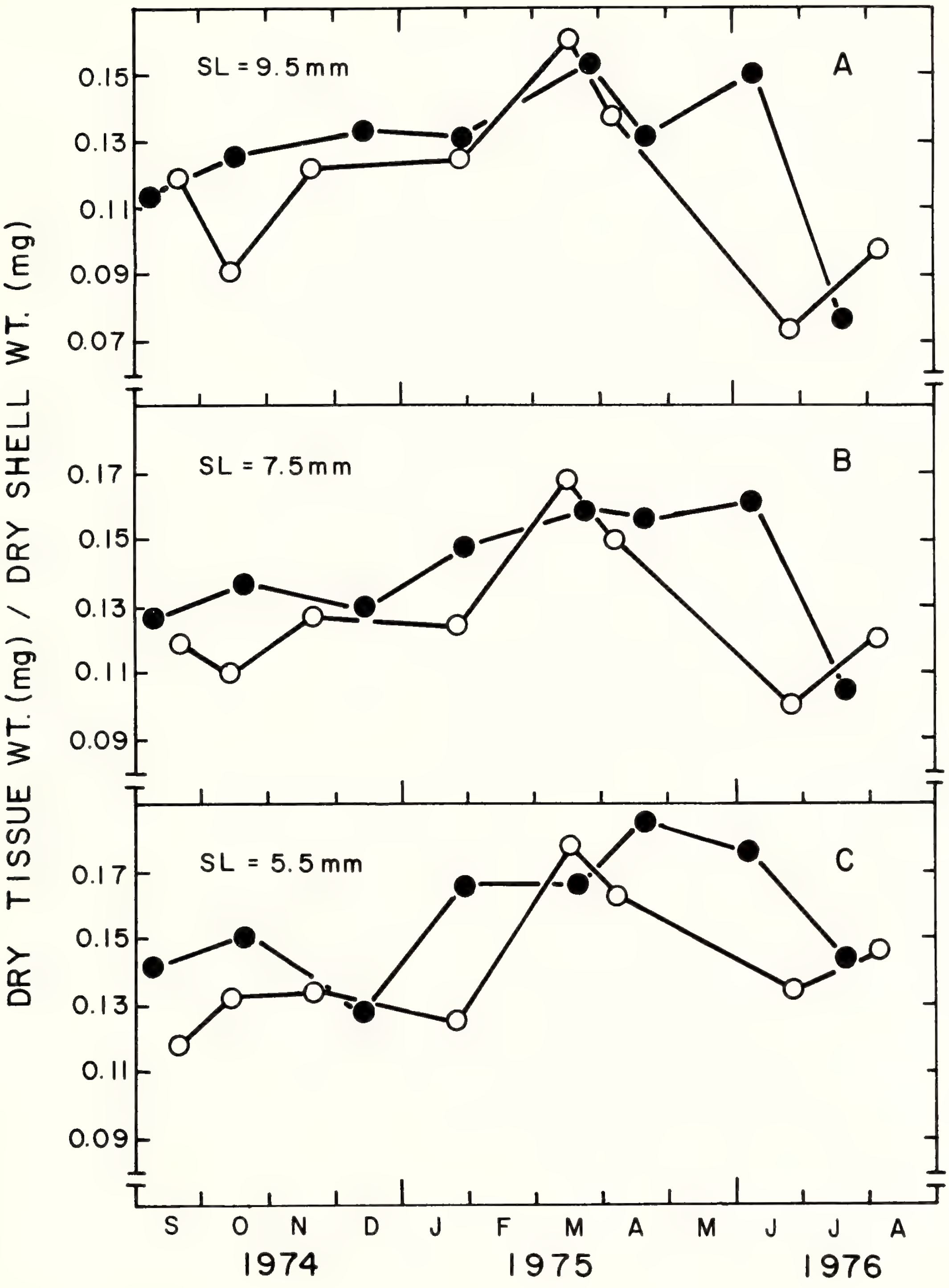

Fig. 3. Effects of thermal effluents on the seasonal variation in dry tissue weight to dry shell weight ratios for populations of *P. virgata virgata* in Lake Arlington. Vertical axis is ratio of dry tissue weight in mg (DTW) to dry shell weight in mg (DSW). Horizontal axis is date of collection in months. Open circles represent DTW:DSW ratios of individuals from an area unaffected by thermal effluents (LAD) and solid circles, individuals from an area receiving thermal effluents (LAOL). **A.** DTW:DSW ratios estimated for an individual with a standard shell length of 9.5 mm. **B.** DTW:DSW ratios estimated for an individual with a standard shell length of 7.5 mm. **C.** DTW:DSW ratios estimated for an individual with a standard shell length of 5.5 mm.

Table 1. Degree of oxygen regulation with progressive hypoxia as expressed by quadratic coefficients ($b_2(10^3)$)[1] from quadratic equations relating standardized oxygen consumption rate (Y) at 25°C to partial pressure of oxygen in torr (X) from full air saturation ($PO_2 = 159$ torr) to the partial pressure at which oxygen uptake ceases ($PO_2 = 0$–9 torr) in the freshwater pulmonate snail, *Physella virgata virgata*, from an area receiving thermal effluents (LAOL) and from an area unaffected by thermal effluents (LAD) (r = correlation coefficient, P = probability level)[2].

LAD					LAOL				
Date	Ambient Water Temperature °C	$b_2(10^3)$	r	Degree of Regulation	Date	Ambient Water Temperature °C	$b_2(10^3)$	r	Degree of Regulation
14 Oct., 1974	23.5	−0.0302	0.944	poor	9 Oct., 1974	28.5	−0.0785	0.976	good
		−0.0690	0.960	moderate			−0.0564	0.950	moderate
		−0.0999	0.954	near perfect			−0.0793	0.869	good
21 Nov., 1974	17.0	−0.0735	0.982	good	31 Jan., 1975	20.5	−0.0601	0.997	moderate
		—	—	—			−0.0782	0.992	good
		—	—	—			−0.0777	0.980	good
25 Jan., 1975	11.5	−0.0533	0.997	moderate	23 Mar., 1975	25.5	−0.0649	0.994	moderate
		−0.0711	0.997	good			−0.0748	0.991	good
		−0.0633	0.995	moderate			−0.0475	0.992	poor
15 Mar., 1975	11.0	−0.0402	0.996	poor	20 Apr., 1975	19.5	−0.0598	0.996	moderate
		−0.0413	0.993	poor			−0.0451	0.996	poor
		−0.0774	0.994	good			−0.0531	0.996	moderate
6 Apr., 1975	15.0	−0.0656	0.996	moderate	9 June, 1976	33.0	−0.0767	0.956	good
		−0.0630	0.988	moderate			−0.0204	0.951	poor
		−0.0681	0.995	moderate			−0.0690	0.958	moderate
26 June, 1976	30.0	−0.0841	0.988	good	20 July, 1976	35.0	−0.0447	0.950	poor
		−0.0719	0.988	good			−0.0552	0.992	moderate
		−0.0096	0.922	non-regulation			−0.0505	0.987	moderate
4 Aug., 1976	32.0	−0.0643	0.981	moderate					
		−0.0496	0.990	poor					
		−0.0808	0.981	good					

[1] $b_2(10^3)$ values relate to the degree of regulation of oxygen consumption rate during progressive hypoxia as follows: < -0.085, nearly perfect regulation; -0.070 to -0.085, good regulation; -0.050 to -0.0699, moderate regulation; -0.020 to -0.0499, poor regulation; and > -0.020, non-regulation (Mangum and Van Winkle, 1973).

[2] n for all regressions is 13 or 14. All regressions are significant at the $P < 0.0005$ level or better.

$\mathring{V}o_2$ was recorded ($t = 0.166$–1.094, $df = 35$, $P < 0.5$). For both populations the critical Po_2, below which $\mathring{V}o_2$ declined proportionately with 0_2 tension, was approximately 70 torr (44% of full air saturation with 0_2) (Fig. 4). When these mean standardized $\mathring{V}o_2$ values were fitted to a quadratic equation versus Po_2 in torr, average $b_2 \times 10^3$ values for the LAD and LAOL populations were -0.0595 and -0.0609, respectively, indicating that overall *P. virgata viragta* is a moderate regulator of $\mathring{V}o_2$ (Mangum and Van Winkle, 1973).

THE RELATIONSHIP BETWEEN $\mathring{V}o_2$ AND DRY TISSUE WEIGHT

For each collection the $\mathring{V}o_2$ values (expressed as μl O_2 (STP) · animal^{-1} · hour^{-1}) recorded for each subsample at each experimental temperature (5°C to 45°C or 50°C in 5°C increments) were transformed into common logarithms and fitted to a linear regression against the logarithmic transformation of subsample mean DTW in mg. The vast majority of these regressions were highly significant (mean r for all regressions = 0.892, mean F for all regressions = 123.8, n = 230, $P < 0.0001$). There were no significant differences between the mean slope values of these regressions between the two sites at any one test temperature ranging from 5° to 45°C ($t = 0.032$–2.04, $df = 21$–25, $P > 0.05$). Nor did they vary significantly with ambient water temperature ($P > 0.05$). Therefore, a grand mean slope value of 0.779 (s.d. = ± 0.279, s.e. = ± 0.018, n = 230) was computed for both populations. This mean slope value falls well within that reported for other aquatic invertebrates (Prosser, 1973).

METABOLIC RESPONSE TO TEMPERATURE

The regressions of $\mathring{V}o_2$ versus DTW for each collection were then utilized to estimate the $\mathring{V}o_2$ of standard individuals with dry tissue weights of 0.94 mg (5.5 mm SL), 2.34 mg (7.5 mm SL) and 5.51 mg (9.5 mm SL). Least

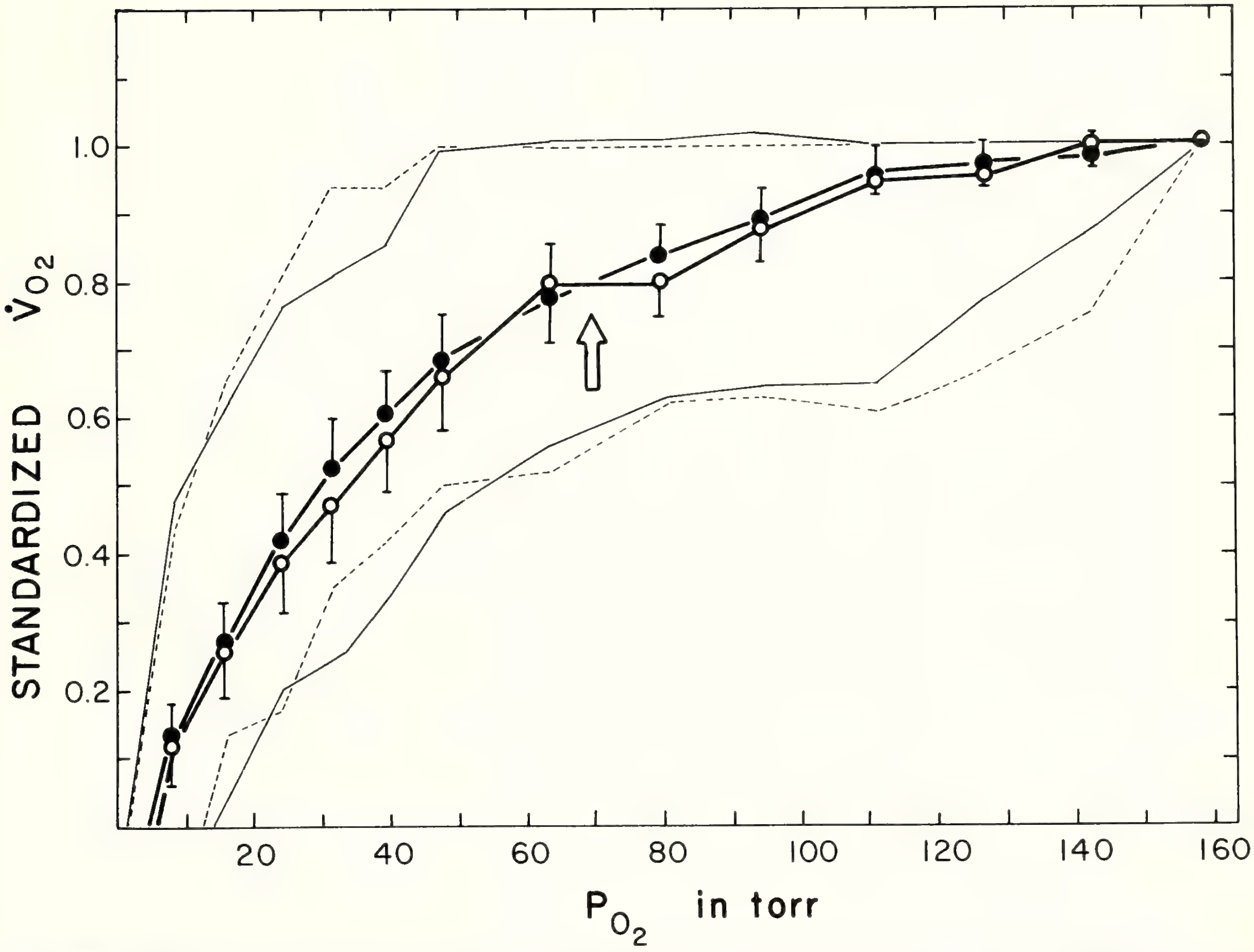

Fig. 4. Mean metabolic response to hypoxia in individuals of *P. virgata virgata* drawn from populations affected and unaffected by thermal effluents in Lake Arlington. Vertical axis is mean standardized oxygen uptake rate ($\mathring{V}_{O_2}$) of all subsamples at 25°C. $\mathring{V}_{O_2}$ was standardized by expressing $\mathring{V}_{O_2}$ of each subsample at any one Po_2 as a fraction of $\mathring{V}_{O_2}$ at full air saturation with 0_2 (Po_2 = 159 torr). Horizontal axis is partial pressure of oxygen (Po_2) in torr (mm Hg). Open circles represent mean standardized $\mathring{V}_{O_2}$ of individuals drawn from LAD population unaffected by thermal effluents and solid circles, that for individuals drawn from LAOL population receiving thermal effluents. Vertical bars about the means represent 95% confidence limits. Solid lines on either side of mean values represent maximum range of $\mathring{V}_{O_2}$ values recorded for LAD specimens, and dashed lines, the maximum range recorded for LAOL specimens. Vertical arrow indicates critical Po_2 of approximately 70 torr at which regulatory ability is lost in individuals from both populations.

squares linear regressions relating the $\mathring{V}o_2$ of a 2.34 mg individual to that of a 0.94 mg or a 5.51 mg individual, respectively, were highly significant ($P < 0.05$) for all test temperatures at each site, indicating that seasonal variation in $\mathring{V}o_2$ was essentially similar in all three standard individuals. Therefore, only the $\mathring{V}o_2$ of the modal 2.34 mg standard individual (which lies very close to the mean DTW of all subsamples used in 0_2 uptake experiments) was utilized in the following analysis of metabolic temperature acclimatization in *P. virgata virgata*.

In both populations the $\mathring{V}o_2$ of a standard individual increased with increasing temperature up to 35°C or 40°C, and, thereafter, declined markedly as the upper lethal limit was surpassed (Figs. 5A–F). The temperature of maximal $\mathring{V}o_2$, roughly equivalent to the maximum tolerated temperature, increased with increased ambient water temperature. Maximal $\mathring{V}o_2$ occurred at 35°C in individuals taken at field water temperatures below 25°C, and increased to 40°C as ambient water temperatures rose above 25°C (Figs. 5A–F). Increases in the temperature of maximal $\mathring{V}o_2$ were associated with an increase in upper thermal tolerance limits (McMahon, 1976a).

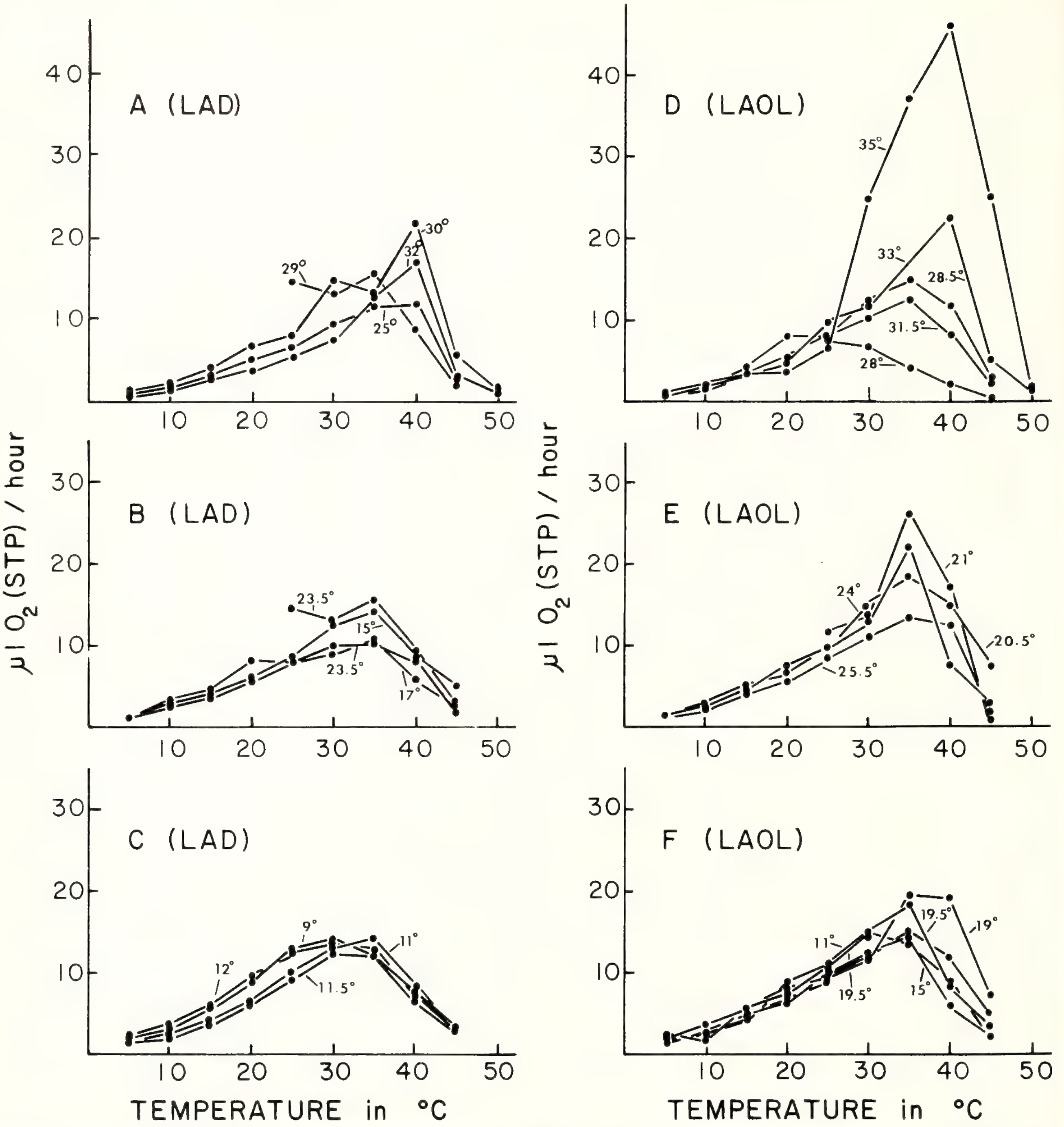

Fig. 5. Metabolic response to acute temperature change in field acclimatized specimens of *P. virgata virgata* from populations affected (LAOL) and unaffected (LAD) by thermal effluents in Lake Arlington. Vertical axis in all figures is oxygen consumption rate ($\mathring{V}_{O_2}$) of a standard 2.34 mg dry flesh weight individual in microliters of oxygen at STP per hour, estimated from log-log linear regressions of $\mathring{V}_{O_2}$ versus dry tissue weight computed from $\mathring{V}_{O_2}$ determinations made for individuals from each collection. Horizontal axis for all figures is test temperature from 5°C to 50°C. Each temperature response curve is labeled with field ambient water temperature recorded at time experimental individuals were collected. **A-C.** Respiratory response to temperatures in field collected individuals from the LAD population unaffected by thermal effluents. **D-F.** Respiratory response to temperature in individuals from the LAOL population receiving thermal effluents.

SEASONAL VARIATION IN Q_{10} VALUES

Q_{10} values relating the response of $\dot{V}o_2$ to temperature change were computed for individual subsamples of *P. virgata virgata* over each 5°C increase in the experimental temperature from 5°C to 45°C. At each 5°C increment in experimental temperature, subsample Q_{10} values for each site were fitted to a least squares linear regression against subsample mean DTW in mg ($n = 6$). Of 214 such regressions computed for the LAD and LAOL populations only 17 (7.9%) showed a significant relationship ($F > 12.2$, $n = 6$, $P < 0.05$) between Q_{10} and DTW, indicating that respiratory response to temperature was not generally correlated with size in this species, allowing mean Q_{10} values to be computed over each increment in experimental temperature from the subsample Q_{10} values determined for each collection. For each 5°C interval in experimental temperature these mean Q_{10} values were fitted to least squares linear regressions against ambient water temperature in °C (Table 2). Ten out of a total of 16 such regressions proved to be significant ($P < 0.05$). Insignificant relationships between Q_{10} and ambient water temperature occurred at increments of 15–20°C and 20–25° C in the LAD poplation and at 5–10°C, 15–20°C, 30–35°C and 40–45°C for LAOL (Table 2).

Significant regressions were utilized to predict Q_{10} values over a series of 5°C increments in ambient water temperature ranging from 10°C to 35°C (Table 3), the approximate range in ambient temperature recorded at both sites (Fig. 2). Mean Q_{10} values were assigned to the entire temperature range when no significant relationship between Q_{10} and ambient water temperature could be demonstrated (Table 3). These estimated Q_{10} values were essentially the same for individuals from the LAD and LAOL populations over the normal ambient water temperature range of 10°C to 35°C and indicated that in *P. virgata virgata* that Q_{10} values decrease as test temperatures increase (Table 3). In contrast, as ambient (field acclimatization) temperature increases, Q_{10} values for any one test temperature increment tend to increase such that over a test temperature range of 5°–35°C the Q_{10} values of individuals acclimatized to 35°C can be more than twice those of individuals acclimatized to an ambient temperature of 10°C (Table 3).

Q_{10} values less than 1.0 are indicative of a decline in $\dot{V}o_2$ with increasing temperature, and associated with the

Table 2. Least squares regression equations relating Q_{10} values of respiratory response to temperature (Y) to ambient water temperature at the time of collection in °C (X) for the freshwater pulmonate snail, *Physella virgata virgata*, from an area receiving thermal effluents (LAOL) and from an area unaffected by thermal effluents (LAD); a = y intercept, b = slope, r = correlation coefficient, n = number of data pairs, F = F statistic, and P = probability level.[1]

Experimental Temperature Range in °C				LAD					
	a	b	r	n	F	P	mean	S.D.	Range
5–10	2.18	0.120	0.669	12	8.12	<0.025*	—	—	—
10–15	2.35	0.067	0.54	12	4.19	<0.10 *	—	—	—
15–20	2.06	0.022	0.22	12	0.50	>0.5	2.65	±0.48	1.93–3.37[1]
20–25	2.21	0.002	0.04	12	0.01	>0.5	2.25	±0.46	1.55–3.32[1]
25–30	0.85	0.066	0.06	14	9.35	<0.025*	—	—	—
30–35	0.50	0.049	0.64	14	8.19	<0.025*	—	—	—
35–40	−0.37	0.059	0.91	14	55.66	<0.0005*	—	—	—
40–45	0.24	−0.005	−0.05	14	3.81	<0.10*	—	—	—

				LAOL					
	a	b	r	n	F	P	mean	S.D.	Range
5–10	−0.40	0.231	0.45	11	2.27	>0.20	5.12	±3.93	2.10–14.83[1]
10–15	1.63	0.112	0.52	11	3.40	<0.10*	—	—	—
15–20	2.78	−0.012	−0.16	11	0.23	>0.50	2.50	±0.55	1.89–3.72[1]
20–25	0.72	0.076	0.59	11	4.75	<0.10*	—	—	—
25–30	−0.25	0.109	0.49	13	3.44	<0.10*	—	—	—
30–35	1.43	0.007	0.10	13	0.11	>0.50	1.59	±0.51	1.05–2.36[1]
35–40	0.15	0.033	0.59	13	5.80	<0.05*	—	—	—
40–45	0.16	−0.001	−0.12	13	0.14	>0.50	0.13	±0.07	0.02–0.25[1]

[1] Mean Q_{10} values, standard deviation of the mean (SD) and range values are supplied for insignificant regressions ($P > 0.10$).
*Indicates that regressions are significant at the $P = 0.10$ level or better.

Table 3. Q_{10} values of respiratory response to temperature at 5°C intervals over an ambient water temperature range of 10–35°C for the freshwater pulmonate snail, *Physella virgata virgata*, from an area receiving thermal effluents (LAOL) and from an area unaffected by thermal effluents (LAD) as estimated from least squares linear regression equations relating Q_{10} to ambient water temperature or from mean Q_{10} values over time in cases of an insignificant ($P > 0.10$) relationship between Q_{10} and ambient water temperatures.

Temperature range in °C	site	Ambient Water Temperature					
		10°C	15°C	20°C	25°C	30°C	35°C
5–10	LAD	3.37	3.96	4.56	5.15	5.75	6.34
	LAOL	5.12*	5.12*	5.12*	5.12*	5.12*	5.12*
10–15	LAD	3.02	3.36	3.69	4.03	4.36	4.70
	LAOL	2.75	3.31	3.49	4.43	4.99	5.55
15–20	LAD	2.65*	2.65*	2.65*	2.65*	2.65*	2.65*
	LAOL	2.50*	2.50*	2.50*	2.50*	2.50*	2.50*
20–25	LAD	2.25*	2.25*	2.25*	2.25*	2.25*	2.25*
	LAOL	1.48	1.86	2.24	2.62	3.00	3.38
25–30	LAD	1.51	1.84	2.17	2.50	2.83	3.16
	LAOL	0.84	1.38	1.93	2.47	3.02	3.56
30–35	LAD	0.99	1.23	1.48	1.72	1.97	2.21
	LAOL	1.59*	1.59*	1.59*	1.59*	1.59*	1.59*
35–40	LAD	0.23	0.52	0.82	1.11	1.41	1.70
	LAOL	0.48	0.65	0.81	0.98	1.14	1.31
40–45	LAD	0.21	0.19	0.16	0.14	0.11	0.09
	LAOL	0.02*	0.02*	0.02*	0.02*	0.02*	0.02*

*Indicates that an insignificant relationship existed between Q_{10} and ambient water temperature ($P > 0.1$), therefore Q_{10} was estimated as the mean value over the entire study period (see Table 2).

onset heat coma in this species as lethal temperatures are approached (McMahon, 1976a; McMahon and Payne, 1980). Individuals from both LAD and LAOL maintain Q_{10} values above 1.0 up to a test temperature of 35°C when taken from field ambient temperatures below 20°–25°C (cold-conditioned). In contrast, individuals conditioned to ambient water temperatures above 20–25°C maintain a Q_{10} above 1.0 (> 0.98) up to a test temperature of 40°C (Table 3). This ability of warm-conditioned individuals to maintain a positive metabolic response to higher test temperatures than can cold-conditioned individuals was associated with a compensatory increase in the upper thermal limit of warm-conditioned individuals.

METABOLIC COMPENSATION FOR SEASONAL TEMPERATURE FLUCTUATION

The elevated Q_{10} values of warm-conditioned individuals are associated with an apparent seasonal compensation of $\mathring{V}o_2$ in *P. virgata virgata*. When the $\mathring{V}o_2$ of a standard 2.34 mg individual (estimated from log-log linear regressions of $\mathring{V}o_2$ versus subsample mean DTW computed from each monthly set of $\mathring{V}o_2$ determinations) are plotted against date of collection for test temperatures ranging between 5°C and 40°C, distinct patterns of seasonal metabolic compensation become apparent (Figs. 6A-H). In both populations the $\mathring{V}o_2$ of a standard individual declines to minimal values during the warmest summer months and is elevated to maximal values during the coldest winter months at test temperatures of 25°C or less (Figs. 6A–E). In contrast, at test temperatures of 30°C or above, there is either no discernable annual pattern of variation in $\mathring{V}o_2$ or there is a marked reversal in the pattern of variation such that peak oxygen consumption rates are recorded in mid-summer and minimal rates occur in mid-winter. This latter pattern was particularly prominent in individuals from the LAOL population (Table 4, Figs. 6F–H).

This distinct pattern of seasonal $\mathring{V}o_2$ variation appeared to be closely associated with seasonal variation in ambient water temperature (Figs. 2 and 6F–H). Least squares linear regressions of the $\mathring{V}o_2$ of a standard individual versus ambient water temperature at the time of collection were significant at $P = 0.1$ or less for both sites at test temperatures of 5°, 10°, 15°, 20°, and 40°C. Significant correlations were also found for LAOL individuals at 25°C. Insignificant correlations ($P > 0.1$) were recorded at 30°, 35° and 45°C for individuals from both sites and at 25°C for individuals from LAD (Table 4).

When tested by Students-t tests for difference between slopes and elevations (Zar, 1974) none of the regressions of $\mathring{V}o_2$ versus ambient water temperature were significantly different at any one test temperature ($P > 0.05$). Nor did a t-test indicate significant differences between mean

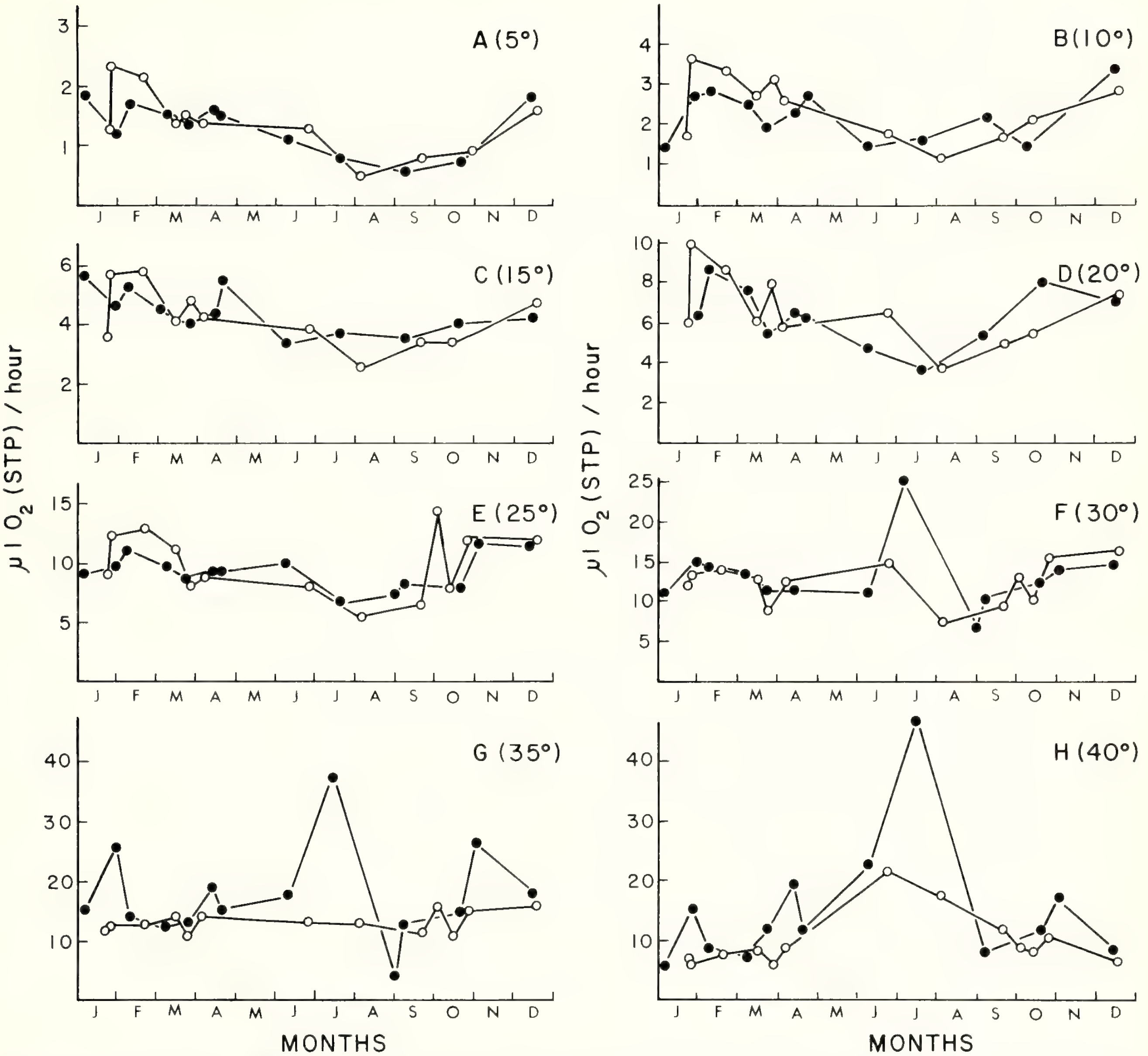

Fig. 6. Seasonal variation of oxygen consumption rate of a standard individual of *P. virgata virgata* from populations affected and unaffected by thermal effluents over test temperatures ranging from 5°C to 45°C. Horizontal axis for all figures is the estimated oxygen consumption rate ($\mathring{V}_{O_2}$) of a standard 2.34 mg dry tissue weight individual in microliters of oxygen at STP per hour. Horizontal axis for all figures is date of collection in months. Open circles represent the $\mathring{V}_{O_2}$ of a standard individual from LAD population unaffected by thermal effluents and solid circles, that of a standard individual from LAOL population receiving thermal effluents. Data are presented for the following test temperatures: **A.** 5°C; **B.** 10°C; **C.** 15°C; **D.** 20°C; **E.** 25°C; **F.** 30°C; **G.** 35°C; and **H.** 40°C.

values of $\mathring{V}o_2$ at specific test temperatures. Therefore, the $\mathring{V}o_2$ values of both populations at each test temperature were combined and fitted to least squares linear regressions versus ambient water temperature at each test temperature. When data from LAD and LAOL subsamples were combined, significant linear relationships ($P < 0.05$) were found between $\mathring{V}o_2$ and ambient water temperature at test temperatures of 5°, 10°, 15°, 20°, 25° and 40°C, while insignificant regressions were recorded at test temperatures of 30°, 35° and 45°C (Table 4, Figs. 7A–H). The slopes of these regres-

Table 4. Least squares linear regression analysis of the weight specific oxygen consumption rate (μl 0_2/(animal • hr)) (Y) of a standard sized specimen of *Physella virgata virgata* (SL = 7.5 mm, dry tissue weight = 2.34 mg) versus field ambient water temperature (X) over a series of experimental temperatures; a = y intercept, b = slope, r = correlation coefficient, n = number of data pairs, F = F statistic and P = probability level. Mean oxygen consumption rates and standard deviations (S.D.) are provided for insignificant ($P > 0.05$) regressions.

Experimental Temperature (°C)	a	b	r	n	F	P	Mean	S.D.
5	2.29	−0.047	−0.78	23	32.1*	<0.001	—	—
10	3.55	−0.059	−0.67	23	16.8*	<0.002	—	—
15	5.88	−0.073	−0.67	23	17.1*	<0.001	—	—
20	9.4	−0.136	−0.70	23	19.6*	<0.001	—	—
25	12.25	−0.130	−0.47	27	7.0*	<0.05	—	—
30	12.70	−0.00003	0.00	27	0.0	>0.50	12.70	±3.37
35	11.46	0.166	0.22	27	1.29	>0.50	15.08	±5.81
40	3.76	0.446	0.48	27	7.61*	<0.05	—	—
45	−0.46	0.204	0.34	27	3.3	>0.20	3.93	±4.62

*Indicates an F statistic larger than the minimum value for a significant regression at the P = 0.05 level or better. Means and standard deviations are not supplied were a significant relationship occurs between oxygen consumption rate and ambient water temperature.

sions were negative at test temperatuares of between 5°C and 25°C (Table 4, Figs. 7A–E) indicating that as ambient field water temperature increases the $\mathring{V}o_2$ of a standard individual decreases which is the more typical pattern of metabolic compensation or acclimation for seasonal temperature variation, referred to as a "type 3" pattern (partial compensation) (Precht, 1958). At test temperatures of 30°C and 35°C there was no distinct correlation of $\mathring{V}o_2$ with ambient water temperature which is indicative of a lack of respiratory compensation for temperature or a "type 4" pattern (no compensation) (Precht, 1958) (Table 4, Figs. 7F and G). At 40°C the slope of the regression of $\mathring{V}o_2$ versus ambient temperature is positive (Table 4, Fig. 7H), indicating that individuals conditioned to warmer ambient temperatures had a higher $\mathring{V}o_2$ than those conditioned to lower temperatures, a pattern which is opposite that of typical metabolic temperature compensation and referred to as "reverse" or "inverse" acclimation (Prosser, 1973), or Precht's (1958) "type 5" curve of metabolic compensation. Although the regression was insignificant ($P > 0.2$) individuals at a test temperature of 45°C also showed a distinct tendency toward reverse acclimation (Table 4, Fig. 7H).

When these regressions of $\mathring{V}o_2$ versus field ambient water temperature (Table 4) are utilized to estimate the $\mathring{V}o_2$ of a standard 2.34 mg DTW individual of *P. virgata virgata* at test temperatures ranging from 5°C to 45°C in 5°C increments over a series of field ambient water temperatures (assumed to represent acclimatization temperatures) ranging from 5°C to 40°C (the range tolerated by natural populations, see McMahon, 1975a, 1976a) the pattern of metabolic temperature compensation in this species becomes evident (Fig. 8). Metabolic compensation for seasonal temperature fluctuation in this species involves a counter clockwise rotation of the oxygen uptake rate-temperature (R-T) curve with acclimatization to increasing field ambient water temperature. The rotation point for the R-T curve appears to lie very near to 30°C where no seasonal metabolic temperature compensation was observed (Figs. 7F and 8), manifested by the insignificant relationship between $\mathring{V}o_2$ and field ambient water temperature at this temperature (Table 4). The slope of the linear regression relating $\mathring{V}o_2$ to ambient water temperature at 30°C was insignificantly different from zero, indicating that field temperature acclimatization had no effect on $\mathring{V}o_2$ at this test temperature (Table 4).

Therefore, when specimens of *P. virgata virgata* are field acclimatized to increasing ambient water temperatures their $\mathring{V}o_2$ decreases at test temperatures below 30°C, a pattern of metabolic temperature compensation typical of many ectothermic species (Precht, 1958) (Figs. 7A–E, 8). In contrast, above a test temperature of 30°C field acclimatization to increasing ambient water temperature induces an increase in $\mathring{V}o_2$ compared to that of specimens conditioned to lower ambient temperatures, a pattern of respiratory compensation characteristic of "reverse" acclimation (Precht, 1958). This counter clockwise rotation of the R-T curve in warm-conditioned individuals is reflected by their elevated Q_{10} values over the entire ambient range of 5°C to 35°C (Table 2 and 3). It is also associated with the elevated $\mathring{V}o_2$ of summer-conditioned individuals at test temperatures above 30°C in both populations (Figs. 6F–H). Such mid-summer elevation of $\mathring{V}o_2$ is particularly conspicuous in the LAOL population, receiving thermal effluents (Figs. 6F–H), where ambient field water temperatures remain above 30°C from June through August (Fig. 2). In this population field acclimatization to temperatures above 30°C appears to induce an extraordinary elevation of $\mathring{V}o_2$ at test temperatures above 30°C (Figs. 5D, 6F–H) and in both populations it is associated with the observed shift in summer-conditioned individuals from a pat-

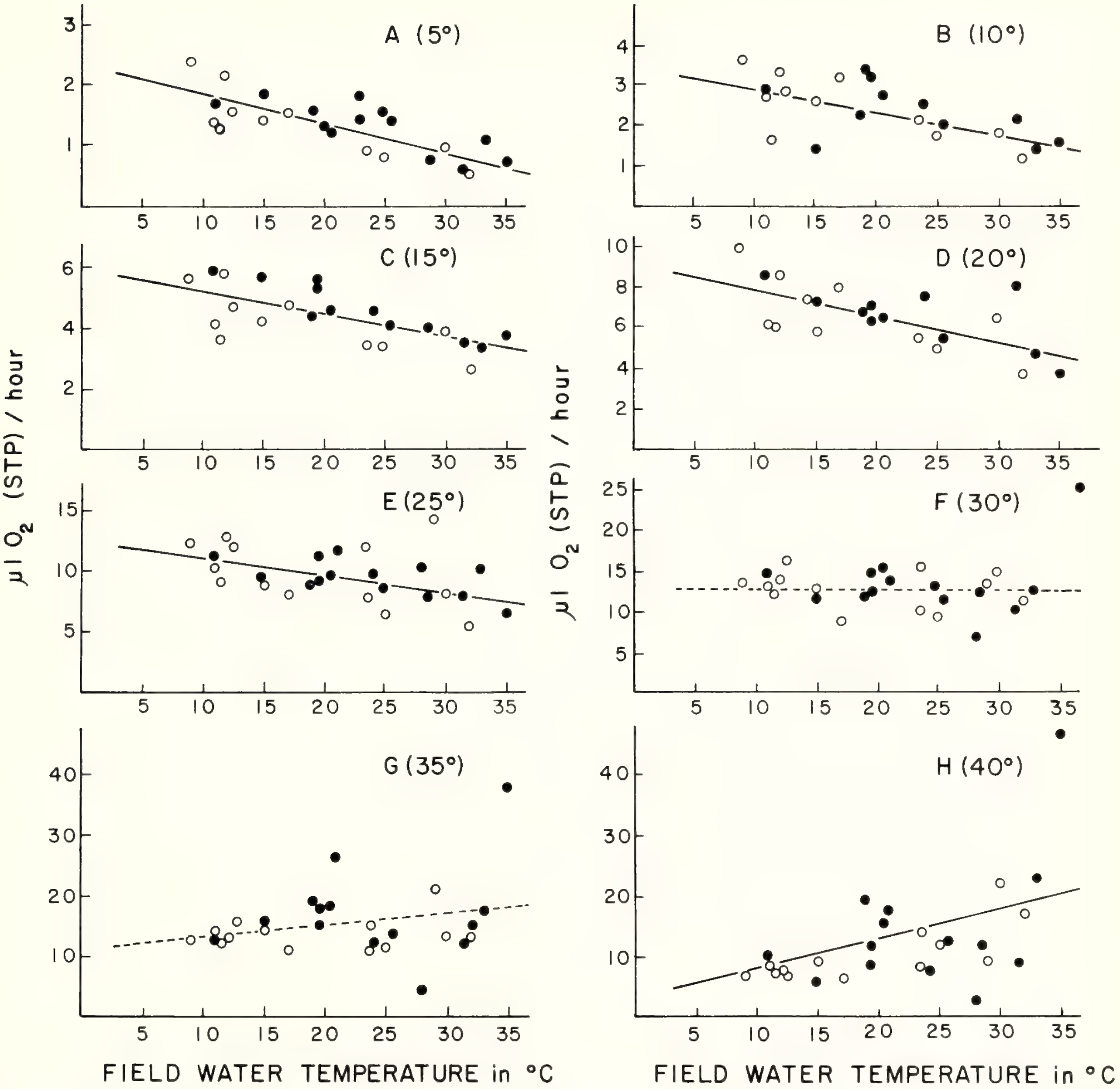

Fig. 7. Effect of field temperature acclimatization on the oxygen consumption rates of *Physella virgata virgata* from Lake Arlington. Vertical axis for all figures is estimated oxygen consumption rate ($\mathring{V}_{O_2}$) of a standard 2.34 mg dry tissue weight individual in microliters of oxygen at STP per hour. Horizontal axis for all figures is field ambient water acclimatization temperature in °C at time of collection. Open circles are $\mathring{V}_{O_2}$ of standard individuals from LAD population unaffected by thermal effluents and solid circles, that of individuals from LAOL population receiving thermal effluents. Solid lines represent best fit of significant ($P < 0.05$) least squares linear regression equations of $\mathring{V}_{O_2}$ versus temperature for combined data from both LAD and LAOL individuals, while dashed lines represent best fits of insignificant ($P > 0.05$) regressions (see Table 4). $\mathring{V}_{O_2}$ data is presented for the following test temperatures: **A.** 5°C; **B.** 10°C; **C.** 15°C; **D.** 20°C; **E.** 25°C; **F.** 30°C; **G.** 35°C; and **H.** 40°C.

tern of partial metabolic temperature compensation (Figs. 7A–E, 8) to one of apparent reverse respiratory acclimation at test temperatures above 30°C (Figs. 7G–H, 8).

The ability of *P. virgata virgata* to compensate $\mathring{V}O_2$ for seasonal temperature variation is incomplete. When the $\mathring{V}O_2$ of a standard individual at test temperatures equivalent to field acclimation temperatures is compared over a wide range of acclimation temperatures, $\mathring{V}O_2$ still increases with

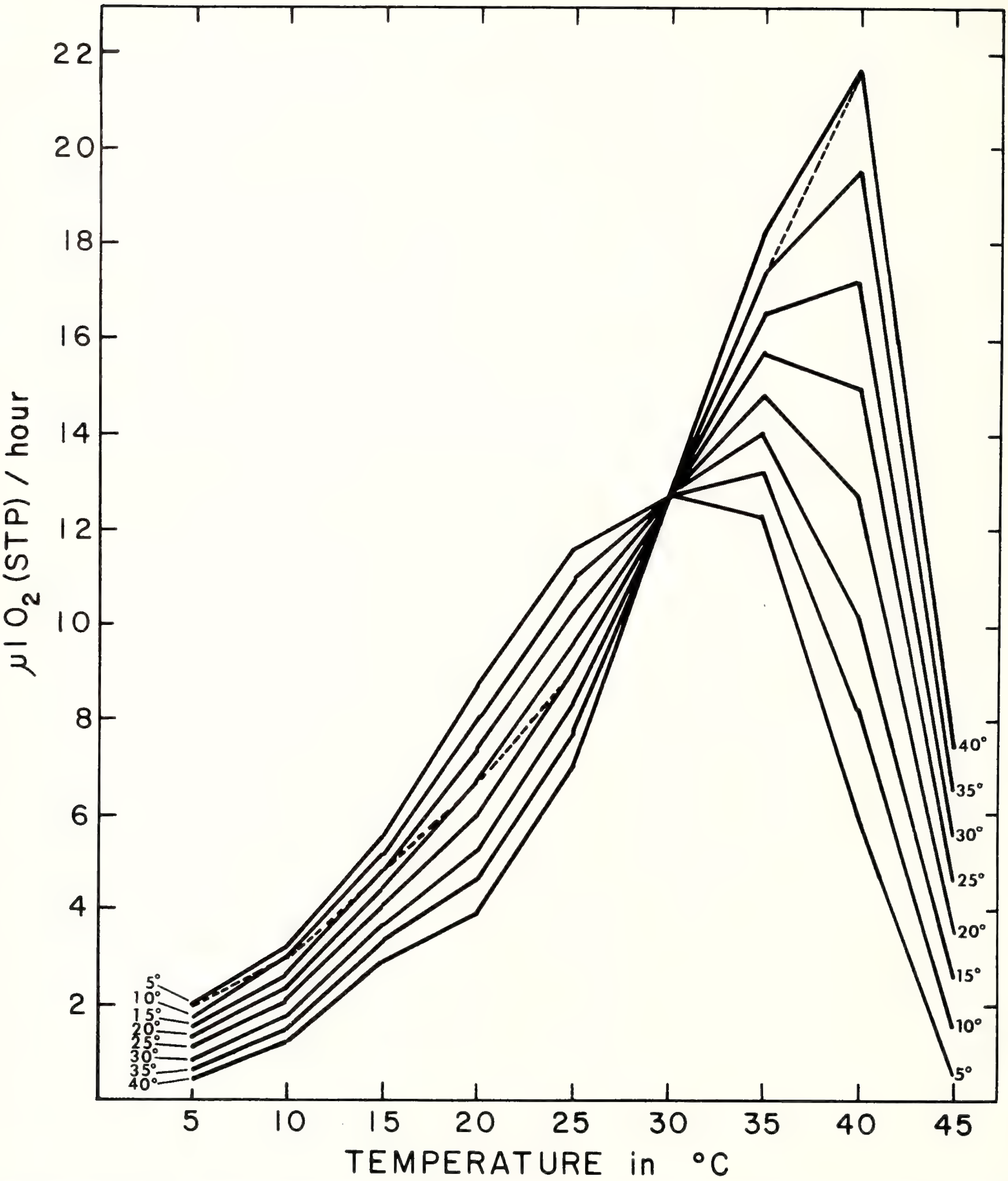

Fig. 8. Oxygen consumption rate of a standard individual of *P. virgata virgata* in response to acute temperature increase from 5°C to 45°C after acclimatzation to field ambient water temperatures ranging from 5°C to 40°C as computed from combined data for the LAD and LAOL populations in Lake Arlington. Vertical axis is oxygen consumption rate ($\mathring{V}_{O_2}$) of a standard 2.34 mg dry tissue weight individual in microliters of oxygen at STP per hour. These $\mathring{V}_2$ values were estimated from linear regressions of $\mathring{V}_{O_2}$ versus field ambient water temperature at the time of collection over an acute test temperature range of 5°C to 45°C for a standard individual acclimatized to ambient temperatures ranging from 5°C to 40°C (see Table 4). Horizontal axis is test temperature in °C. Specific field acclimatization temperature associated with an estimated metabolic response curve to increasing test temperature is indicated in °C at either end of the appropriate rate-temperature curve. Note that the sharp decline in $\mathring{V}_{O_2}$ at test temperatures above 35°C or 40°C is associated with the onset of heat coma in this species. Dashed line indicates estimated respiratory response to temperature of an individual field acclimatized to entire range of sublethal test temperatures from 5°C–40°C.

increasing temperature (Fig. 8). This partial acclimation (Type 3 curve, Precht, 1958) is reflected by the relatively high respiratory Q_{10} values of standard specimens (DTW = 2.34 mg) of *P. virgata virgata* acclimatized over the entire range of sublethal test temperatures (5°–40°C) (Fig. 8). These Q_{10} values for acclimatized individuals are as follows: 5°–10°C = 2.06; 10°–15°C = 2.62; 15°–20°C = 1.94; 20°–25°C = 1.82; 25°–30°C = 1.99; 30°–35°C = 1.84; and 35°–40°C = 1.56. Q_{10} values approaching one are characteristic of complete respiratory temperature compensation (Precth, 1958; Prosser, 1973). As the Q_{10} values of acclimated specimens of *P. virgata virgata* are considerably lower than that of unacclimated individuals below 30°C (Table 3), but do not approach one, this species appears capable of only relatively limited or partial temperature compensation of metabolic rate over most of its ambient temperature range.

DISCUSSION

The majority of extensive studies of seasonal variation and acclimatization of oxygen consumption in freshwater pulmonates (for a review see McMahon, 1983) have focused on the highly advanced Ancyloplanorbid limpets (Berg, 1952; Berg, et al., 1958; Burky, 1971; Calow, 1975; McMahon, 1973; Wood, 1978). Only a relatively few such studies have been completed for more primitive lymnaeids or physids (Berg and Ockelmann, 1959; Daniels and Armitage, 1969). Thus, while our knowledge of the respiratory adaptations of advanced, highly aquatic basommatophoran freshwater snails is relatively extensive, there is little information of this sort for basommatophoran groups as the Physidae which are less adapted for a purely aquatic schesis, retain the mantle cavity as an air breathing lung, and presumably, more closely resemble the primitive ancestral basommatophoran stock in their respiratory physiology.

RESPONSE TO HYPOXIA

P. virgata virgata was a moderate regulator of $\mathring{V}o_2$ during progressive hypoxia (Fig. 5). Its $b_2 \times 10^3$ value (Mangum and Van Winkle, 1973) of approximately -0.060 and critical Po_2 of 70 torr (Fig. 5) fall in the lower half of the range of values for other freshwater basommatophoran species (Berg, 1952; Berg and Ockelmann, 1959; McMahon, 1973; von Brand and Mehlman, 1953), which on the whole are relatively good regulators of $\mathring{V}o_2$ (for a review see McMahon, 1983). The regulatory ability of *P. virgata virgata* is similar to that of the European species, *Physa fontinalis* (L.) ($b_2 \times 10^3 = -0.0758$, McMahon, 1983). Somewhat surprisingly, the regulatory ability of *P. virgata virgata* and of other pulmonates is generally much greater than that of freshwater prosobranch snails, which are nearly all poor to non-regulators of $\mathring{V}o_2$ (Akerlund, 1974; Berg, 1961; Berg and Ockelman, 1959; Hawkins and Ultsch, 1979; Lumbye, 1958; Studier and Pace, 1978), with the single exception of *Valvata piscinalis* (Müller) which is a moderate regulator ($b_2 \times 10^3 = -0.0628$) (Berg and Ockelmann, 1959; McMahon, 1983).

The relatively well developed regulatory ability of *P. virgata virgata* and other freshwater pulmonates may be an adaptation to their warm, shallow, often eutrophic, periodically hypoxic habitats (McMahon, 1983). In such environments the capacity for periodic aerial gas exchange at the water surface and a relatively well developed ability to regulate aquatic $\mathring{V}o_2$ would be highly adaptive. Such is certainly the case with *P. virgata virgata* which is found commonly in Texas aquatic habitats with low oxygen concentrations and high B.O.D.'s (McMahon, unpublished observations). In contrast, freshwater prosobranchs appear to be generally limited to deeper, well oxygenated, oligotrophic freshwater habitats where the ability to regulate $\mathring{V}o_2$ would confer no selective advantage (Aldridge, 1983; McMahon, 1983).

Among the Ancyloplanorbids, the ancylid limpet, *Laevapex fuscus* (C. B. Adams), has been shown to display a distinct seasonal variation in its ability to regulate $\mathring{V}o_2$. In the summer warm-conditioned individuals are poor regulators of $\mathring{V}o_2$ while cold-conditioned, winter individuals tend towards near-perfect regulation of $\mathring{V}o_2$ (McMahon, 1973). This increase in regulatory ability was induced by declining temperature and thought to compensate for the low Po_2 of its overwintering habitat in reducing sands and muds (McMahon, 1973, 1975b). Indeed, many species of the Ancyloplanorbidae overwinter buried in substrata of low Po_2 (Boerger, 1975; Clampitt, 1972; Rowan, 1966; Streit, 1978). In contrast, *P. virgata virgata* does not enter reducing substrata to overwinter. Instead, this species (McMahon, 1975a, 1976a), as do other species of Lymnaeids and Physids, migrates to deeper offshore waters (depth > 0.5 m) where it overwinters on hard surfaces directly exposed to water of relatively high Po_2 (Boag and Bentz, 1980; Cheatum, 1934; Clampitt, 1970, 1974; DeWitt, 1955; Russell Hunter, 1953). Therefore, in the relatively well oxygenated overwintering habitat of *P. virgata virgata* a cold-induced increase in the regulation of oxygen consumption would be of little selective value.

METABOLIC RESPONSE TO TEMPERATURE

The respiratory Q_{10} values of the majority of basommatophoran species fall below 2.5 (McMahon, 1983). In contrast, respiratory Q_{10} values for *P. virgata virgata* are generally greater than 2.5 within the normal ambient temperature range of 5°C to 30°C (Table 3). The elevated Q_{10} values of *P. virgata virgata* indicate that it exercizes much less control over its metabolic rates than do the majority of freshwater pulmonate species (McMahon, 1983). This species shallow freshwater habitats in the southwestern United States are characterized by wide diurnal temperature fluctuations. Its high Q_{10} values indicate that it also must have a wide diurnal variation in activity, being highly active during periods of maximal mid-day water temperatures and least active during evening periods of minimal water temperatures.

SEASONAL TEMPERATURE COMPENSATION OF UPPER THERMAL LIMIT

The ability of *P. virgata virgata* to compensate its upper temperature tolerance limit for seasonal temperature fluctuation is reflected by the increase in the temperature of maximum $\mathring{V}o_2$ from 35°C to 40°C (Figs. 6A–F) and the increase in Q_{10} values at 35°C to 40°C and 40°C to 45°C (Table 3) with increasing field acclimatization temperature. This compensatory increase the temperature of metabolic suppression is associated with an increase in upper thermal limit measured as heat coma temperature from 38°C to 42°C in 10°C acclimated specimens to 44°C to 46°C in 30°C acclimated specimens from the LAD and LAOL populations, respectively (McMahon, 1976b). The high correlation between the temperature of heat coma and of metabolic suppression indicates that heat coma may be partially associated with the inhibition of cellular aerobic metabolism and/or with the mechanisms of gas exchange and circulation.

SEASONAL TEMPERATURE COMPENSATION OF METABOLIC RATES

The wide interspecific variation in patterns of seasonal metabolic temperature compensation among freshwater basommatophorans (McMahon, 1983) suggest that such responses may have been independently evolved under the specific selection pressures associated with the microhabitat temperature regime of any one phyletic group. The majority of species tested, including *P. virgata virgata,* display the more typical pattern of partial metabolic compensation in which the $\mathring{V}o_2$ of cold-conditioned individuals is greater than that of warm-conditioned individuals at any one test temperature (Berg and Ockelmann, 1959; Beames and Lindeborg, 1967; Daniels and Armitage, 1969; Calow, 1975; Woods, 1978; Meakins, 1980). In *P. virgata virgata* and the other species tested, metabolic temperature compensation (compensation curve type 3, Precht, 1958), allows only partial seasonal regulation of metabolic rate (McMahon, 1983). Such partial metabolic temperature compensation characterizes most invertebrates (Prosser, 1973). However, the capacity of *P. virgata virgata* for metabolic temperature compensation appears particularly underdeveloped, as was indicated by the high respiratory Q_{10} values of field acclimatized individuals when compared across ambient acclimatization temperatures (Q_{10} range = 1.56 (35°–40°C) – 2.62 (10°–15°C) (Fig. 8). This range of Q_{10} values for field acclimatized specimens of *P. virgata virgata* is generally even greater than that reported for unacclimatized individuals of other pulmonate species (McMahon, 1983).

The adaptational significance of the reduced capacity of *P. virgata virgata* to regulate $\mathring{V}o_2$ in response to acute temperature variation and to compensate rates for seasonal temperature variation is unclear. This species, while relatively inactive during the colder parts of the year, continues to locomote and graze during overwintering periods (McMahon, unpublished observations). During the winter, algal productivity in Lake Arlington is reduced (Carr, 1973; Peeler, 1980), as is the standing crop of periphyton or *Awfwuchs* on which this species grazes (Hopkins and McMahon, 1979). Under such conditions, overwintering specimens of *P. virgata virgata* may survive on organic energy stores which would be conserved by a large, cold-induced reduction in its metabolic rate. Its limited metabolic compensatory ability may provide only the relatively small increase in metabolic rate required for overwintering individuals to maintain essential functions, radular activity, limited locomotion and position on the substratum.

Metabolic temperature compensation in *P. virgata virgata* is characterized by a counter clockwise rotation of the R-T curve about a pivot point lying very near to 30°C with increasing acclimatization temperature (Fig. 8). This form of metabolic temperature compensation is common in ectothermic animals (Prosser, 1973) and involves not only a decrease in the metabolic rate of warm-conditioned individuals at test temperatures below the pivot point temperature, characteristic of the more typical pattern of temperature acclimation, but, also, an increase in the metabolic rate of warm-conditioned individuals above the pivot point temperature (Fig. 8), characteristic of "reverse" or "inverse" acclimation (Precht, 1958; Prosser, 1973). It is interesting to note that the 30°C pivot point approximates the maximum, ambient, mid-summer water temperature of the natural Texas freshwater habitats of *P. virgata virgata* (Aldridge and McMahon, 1978; McMahon, 1975a, 1976a, 1976b; McMahon and Williams, 1985; and Fig. 2). Consequently, individuals rarely experience ambient temperatures that could cause excessive and presumably energetically inappropriate increases in $\mathring{V}o_2$ as occur in warm-conditioned specimens of *P. virgata virgata* at field ambient temperatures above 35°C (Fig. 8). Such elevated ambient temperatures generally only occur in hot springs (Issel, 1908; Brues, 1928; Beames and Lindeborg, 1967) or areas receiving industrial thermal effluents (Agersborg, 1932; McMahon, 1975a, 1976a, 1976b; Sankurathri and Holmes, 1976; Wood, 1978). In mid-summer the LAOL population of *P. virgata virgata* (exposed to thermal effluents) experienced temperatures well above 30°C in the Hot Pond (Fig. 2), which caused their $\mathring{V}o_2$ to be greatly elevated at test temperatures above 30° C compared to that of LAD individuals, which rarely experienced ambient temperatures above 30° C (Figs. 5D, 6F–H).

The highly elevated metabolic rates of summer-conditioned LAOL individuals may have reduced the assimilated energy available for growth and reproduction in mid-summer compared to those of the LAD population. Indeed, when ambient water temperatures at the LAOL site rose above the 30°C limit, beyond which $\mathring{V}o_2$ becomes greatly elevated (Fig. 8), from early July through mid-October (Fig. 2), individual growth rates were reduced compared to that of the LAD population (McMahon, 1975a). In addition, the number of eggs per egg mass oviposited by individuals of the LAOL *P. virgata virgata* population was also significantly reduced during this period (LAOL, mean eggs/egg mass = 11.3; LAD, mean eggs/egg mass = 17.4) (McMahon, 1975a).

If artificially elevated water temperatures can induce major shifts in the allocation of assimilated energy between maintanence and production as appears to occur in the LAOL *P. virgata virgata* population, then the long-term effects of thermal discharges at sublethal temperatures may be just as deleterious to natural populations of aquatic organisms as discharges at lethal temperatures. Such discharges could cause severe reductions in growth, and reproductive capacity and increases in time to maturity below the limits required for replacement equilibrium and eventually lead to the long-term extinction of populations isolated in areas receiving thermal effluents. Such a possibility, argues strongly for the basing of thermal discharge standards, not on the upper lethal limits of effected species as is generally practiced (for reviews and examples see Gibbons and Sharitz, 1974; Hart and Fuller, 1974; Esch and McFarlane, 1976 and references therein), but, rather, on studies of the long-term effects of artificially elevated temperatures on the growth, reproductive rate and bioenergetic partitioning of effected species and populations as those of van der Schalie and Berry (1973) and Mattice (1976) for freshwater snails.

ADAPTIVE VALUE OF RESPIRATORY COMPENSATION

Previously accepted hyptheses regarding the concept of metabolic compensation for temperature have been recently questioned. It has been suggested that an elevated standard metabolic rate in cold-conditioned individuals implies an energetically wasteful and, therefore, non-adaptive increase in maintenance energy (for a review see Parry, 1984). Parry (1978, 1983, 1984) has presented an alternative hypthesis for observed seasonal variation in the oxygen consumption rates of ectothermic animals, which suggests that seasonal changes in metabolic rate are associated with variation in growth or biosynthesis rate, rather than direct compensation for long-term temperature fluctuation. It is suggested that cold-acclimatized individuals have a greater potential for growth than warm-acclimatized individuals. As such, they display an elevated growth (biosynthesis) rate which is associated with an elevated $\mathring{V}o_2$ at any one test temperature. Therefore, if maintenance energy at any one test temperature remains constant throughout the year, and that involved with biosynthesis is dependent on growth rate, the metabolic rate of faster growing, cold acclimatized individuals will be greater than that of slower growing, warm acclimatized individuals (Parry, 1978, 1983, 1984). While there appears to be little question that increased biosynthesis has an energetic cost manifested by an increase in metabolic rate, it does not appear to be the major cause of seasonal metabolic variation in *P. virgata virgata*. Summer-conditioned specimens of this species feed on peak standing crops of *Aufwuchs,* and display both maximimal growth rates (McMahon, 1975a) and maximal flesh weights (Fig. 3A–C) indicative of high levels of biosynthesis. However, their $\mathring{V}o_2$ was lower over the normal ambient temperature range (5°–30°C) than that of winter-conditioned individuals feeding on minimal standing crops of *Aufwuchs* (Hopkins and McMahon, 1979) and displaying depressed growth rates (McMahon, 1975a) and flesh weights (Fig. 3A–C). Therefore, the observed seasonal changes in $\mathring{V}o_2$ did not appear to be directly correlated with variation in biosynthetic rate in this species. Instead, the partial compensation of $\mathring{V}o_2$ observed in cold-conditioned individuals may reflect the increased metabolism required at low temperatures to generate the minimal amount of muscular activity to remain attached to the substratum, locomote, and sustain radular feeding at levels which would supply at least a portion of metabolic energy demands. In this sense, the classic view of metabolic compensation to cold temperatures may be adaptive if the increase in the rate of energy aquisition generated (by allowing feeding activity to be sustained) is proportionately greater than the resultant compensatory increase metabolic rate. Non-compensation of metabolic rate could reduce the efficiency of energy ingestion and assimilation to less than maintenance levels that would require utilization of organic energy stores to support maintenance metabolism, leading to tissue degrowth in overwintering individuals (Russell-Hunter, et al., 1984). In such cases, there should be a strong selective pressure for "reverse" acclimation which minimizes metabolic rate in inactive, non-feeding, overwintering individuals. Indeed, this function has been assigned to reverse metabolic temperature compensation in a number of freshwater and marine molluscan species (Burky, 1971; McMahon and Russell-Hunter, 1981; McMahon and Wilson, 1981). The above hypothesis also suggests that reduction of maintenance energy levels in warm-acclimated individuals would be adaptive it allowed greater allocations of assimilated energy to growth and reproduction (Russell-Hunter and Buckley, 1983).

Metabolic temperature compensation may be of very low adaptive value in ectothermic species inhabiting environments characterized by high levels of short-term temperature instability such as intertidal regions, as it would provide no long-term increase in metabolic efficiency. Indeed, many species of intertidal molluscs show little or no apparent metabolic compensation for temperature (Kennedy and Mihursky, 1972; Bayne, et al., 1973; McMahon and Wilson, 1981; Shumway and Koehn, 1982). In contrast, metabolic temperature compensation may be of much greater adaptive value to species such as *P. virgata virgata* from aquatic habitats with more predictable temperature regimes in which seasonal temperature variation is distinctly greater than diurnal temperature variation. In such habitats metabolic temperature compensation could greatly increase the efficiency of energy allocation to growth and reproduction.

The majority of studies of seasonal metabolic acclimatization in freshwater molluscs involve repeated determinations of $\mathring{V}o_2$ at a single test temperature or over a relatively narrow range of temperatures in the upper portion of a species' normal ambient range. Only two investigations of metabolic temperature compensation in fresh water gastropods have involved test temperatures extending over the entire ambient range. These studies demonstrated that in both *Helisoma trivolvis* (Say) (Wood, 1978) and *P. virgata virgata* (this study), respiratory acclimatization to warm temperatures involved a counter clockwise rotation of R-T curves (involving an increase in Q_{10}) about a temperature lying near the upper end of the normal range. If such R-T curve rotation is common among freshwater pulmonates, determinations of seasonal variation in $\dot{V}o_2$ at test temperatures near the upper portion of a species' ambient range could not only greatly underestimate a species' capacity for metabolic compensation, but, in the extreme case, result in an apparent pattern of non- or "reverse" metabolic temperature compensation of no real adaptational significance.

RESPIRATORY ADAPTATION TO THERMAL EFFLUENTS

The elevated temperatures of habitats receiving thermal effluents have been shown to select for genetically differentiated physiological races characterized by increased thermal tolerance limits in a number of species. Thermally tolerant races of both freshwater fish (Holland, et al., 1974; Murphy, et al., 1976) and pulmonate snails (McMahon, 1976a) have been reported in environments receiving thermal effluents. After 18 years (54 generations) of isolation in an area receiving thermal effluents the upper thermal tolerance limit of the LAOL *P. virgata virgata* population was 2°C higher than that of thermally unaffected LAD population. Therefore, these two populations appeared to be genetically different physiological races (McMahon, 1976a). It was somewhat surprising then, that the present investigation revealed no significant differences in the routine metabolic rates of these two populations, either in response hypoxia, temperature, or seasonal metabolic compensation, indicating that no metabolic adaptations to elevated temperature had been evolved in the LAOL population. Indeed, the entire concept of metabolic temperature adaptation has been recently questioned. Carefully controlled experiments have shown that cold-adapted arctic and antarctic ectothermic species do not have elevated standard metabolic rates compared to warm-adapted temperate and tropical species as previously reported (Clarke, 1980; Holeton, 1974). Similarly, metabolic temperature adaptation does not appear to occur in animal populations isolated in thermal effluents. In the two species of fresh water snails, *H. trivolvis* (Wood, 1978) and *P. virgata virgata*, for which such information exists, no differences in routine metabolic rate, metabolic response to acute temperature variation or the pattern of seasonal metabolic compensation could be detected between natural and thermally affected populations after isolation in habitats receiving thermal effluents for nearly 20 years or 60 generation (each species was reported to have three generations per year, McMahon, 1975a; Wood, 1978).

The lack of physiological race formation by the LAOL population in its metabolic responses to hypoxia is understandable as the high rate of water circulation through discharge areas prevents significant decreases in effluent ambient oxygen concentrations (Bible, 1983). Under such conditions ambient Po_2 is actually elevated above ambient source levels in warmed discharge waters.

The lack of physiological race formation in freshwater snail populations isolated in thermal discharge areas with regard to both metabolic rate and seasonal metabolic temperature compensation for seasonal temperature variation is less easy to comprehend. It is possible that the 5°C–10°C elevation in discharge water temperatures (McMahon, 1975a, 1976a, Wood, 1978, this study) is not sufficient to select for individuals with reduced metabolic rates or forms of metabolic temperature compensation adapted to elevated temperatures (for example, an elevation in the pivot temperature for the compensatory rotation of R-T curves). Indeed, an artificial 5°–10°C increase in ambient temperature may have relatively little impact on species such as *H. trivolvis* and *P. virgata virgata* which encounter extensive temperature variation in their natural shallow freshwater environments. In shallow Texan fresh waters annual ambient temperature variation can be greater than 35°C and diurnal temperature variation greater than 15°C (McMahon, 1975a, 1976a, 1976b, 1983, unpublished observations).

Alternatively, the evolution of a physiological race with reduced maintenance energy demands and/or different patterns of seasonal metabolic compensation may involve relatively large amounts of genetic information making it resistant to the short-term selective pressures associated with heated effluents while adaptation of upper thermal tolerance limits may involve selection for alleles coding for isozymes with increased efficiencies at elevated temperatures in only a relatively few key enzyme loci associated with nervous system function which appears to be most sensitive to heat induced failure in molluscs (Hamby, 1975; McMahon, 1976a; McMahon and Payne, 1980). If the selection pressure for a thermally tolerant race involves relatively few alleles and loci it may allow the short-term development (less than 60 generations) of thermally tolerant races isolated in heated effluents as reported for the LAOL *P. virgata virgata* population in Lake Arlington (McMahon, 1976a). In comparison, the enzyme systems controlling metabolism may be far more extensive. As such, respiratory enzymes appear to be generally conservative with regard to temperature selection (Somero, 1975; Powell, 1976). Such large amounts of genetic material may be relatively resistant to temperature selection, as whole suites of mutually compatable alleles may have to be concurrently selected to produce significantly adaptive phenotypic changes in the control of metabolic rate. If the chances of an adaptive phenotype appearing in any one individual are extremely low, the formation of metabolically adapted races in areas receiving thermal effluents is highly unlikely. Indeed, as anarctic ectothermic species are reported to lack metabolic temperature adaptation after an entire evolutionary history in extreme cold (Holeton, 1974; Clarke, 1980), it seems highly unlikely that metabolic adaptations to elevated temperatures would evolve in species such as *P. virgata virgata* that have been isolated in thermal effluents for only a relatively few generations.

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SEASONAL VARIATION IN OXYGEN CONSUMPTION RATES, NITROGEN EXCRETION RATES AND TISSUE ORGANIC CARBON: NITROGEN RATIOS IN THE INTRODUCED ASIAN FRESHWATER BIVALVE, *CORBICULA FLUMINA* (MÜLLER) (LAMELLIBRANCHIA: CORBICULACEA)

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Specimens of *Corbicula fluminea* were collected monthly from May 1981, through December 1982, in an inlet of Lake Arlington, Tarrent County, Texas, from which an electrical power station drew raw cooling water. Specimens carried by intake currents onto travelling screens in front of the cooling water intake embayments were also collected. Specimens were either maintained in 1.0l jars at field ambient water temperature prior to experimentation or were frozen at −74° C.

Within 24 h of collection the oxygen uptake rates ($\mathring{V}O_2$) of subsamples of 10 individuals or groups of smaller individuals with shell lengths (SL) chosen to be representative of SL range in the adult population (adult SL $>$ 10 mm) where monitored with oxygen electrodes. $\mathring{V}O_2$ for inlet specimens was determined at ambient temperature, 15° C and 25° C. $\mathring{V}O_2$ for travelling screen specimens was determined only at ambient water temperature. Ammonia nitrogen excretion rates ($\mathring{V}N_2$) were similarly monitored in individuals of both the inlet population and the travelling screens with an ammonia electrode. For each collection the tissue dry weight (DTW), shell dry weight (SDW), tissue organic carbon content (utilizing a wet oxiation method) and tissue nitrogen content (utilizing a micro-Dumas combustion method) were determined for subsamples of 10 previously frozen individuals of a size range representative of the natural population.

A minimal DTW:DSW ratio of 0.03:1 was recorded in both inlet and travelling screen specimens during the spawning period from June through September. The DTW:DSW ratio increased throughout the winter and spring, reaching a maximum of 0.06:1 in late May just prior to spawning. The summer decline in the DTW:DSW ratio represented a 50% reduction in DTW during spawning. The DTW:DSW ratio of travelling screen specimens was significantly ($P < 0.05$) lower than that of inlet specimens. Tissue organic carbon and nitrogen contents were greatest in overwintering individuals, least in spawning individuals and significantly reduced ($P < 0.05$) in travelling screen specimens. Tissue organic carbon: tissue nitrogen (C:N) ratios ranged from 5:1 to 6:1 in the inlet population, corresponding to a tissue protein content of 83–89% of DTW and displayed no distinct seasonal variation. The C:N ratio of travelling screen specimens was significantly reduced ($P < 0.05$) ranging from 4:1 to 5:1, equivalent to a protein content of 89–95% DTW.

The pattern of seasonal variation in $\mathring{V}O_2$ (μl O (STP)/hr) was similar in all size classes. At ambient water temperatures maximal summer $\mathring{V}O_2$ values were 10 fold greater than minimal mid-winter values. Field-conditioned specimens showed reverse or inverse respiratory compensation for temperature associated with an increase in the $\mathring{V}O_2$ of individuals at test temperatures of 15° and 25° C when conditioned to increased field ambient water temperatures. Reverse respiratory compensation in *C. fluminea* was associated with a counter-clockwise rotation of the rate-temperature (R-T) curve around a pivot point of $\approx$0° C in warm-conditioned specimens. Rotation of the R-T curve resulted in a doubling of respiratory Q_{10} values in summer-conditioned individuals ($Q_{10} \approx 3.0$) compared to winter-conditioned specimens ($Q_{10} \approx 1.5$). Reverse acclimation in *C. fluminea* may conserve overwintering energy stores and prevent energetically wasteful increases in metabolic rate during short-term increases in winter water temperatures.

Determined at field ambient water temperatures, $\mathring{V}N_2$ (μl N_2 (STP)/hr) was 40 fold greater in summer-conditioned individuals than in winter-conditioned individuals. Thus, the

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relative degree of annual variation in $\mathring{V}N_2$ was four times greater than that of $\mathring{V}O_2$. The $\mathring{V}N_2$ of travelling screen individuals was significantly greater ($P < 0.05$) than that of the inlet population.

The greater annual variation of $\mathring{V}N_2$ relative to $\mathring{V}O_2$ indicated that *C. fluminea* undergoes major seasonal shifts in protein catabolism. The molar ratio of oxygen consumed to nitrogen excreted (O:N) ranged between 50:1 and 900:1 in winter-conditioned specimens, representative of a catobolism almost completely dominated by the degradation of non-nitrogenous organic compounds (lipids and carbohydrates). At the onset of ctenidial incubation of embryos in late May, O:N fell to 5:1 to 10:1 where it remained until late fall, representative of a catabolism almost completely dominated by protein degradation. This shift to a protein dominated catabolism in spawning individuals is associated with a 50% reduction in tissue biomass and may be the result of a massive transferral of ingested carbohydrates and lipids to egg production. During the winter increase in tissue and gonad biomass, assimilated amino acids appear to be diverted into anabolic processes marked by a 10 to 20 fold increase in O:N.

O:N ratios of travelling screen specimens were significantly lower (range ≈ 4:1 to 40:1) than those from the inlet population, indicating that they were more dependent on protein degradation for maintenance of metabolic rates. The low O:N ratios and low tissue biomass of travelling screen specimens indicated depletion of organic energy stores and partial dependence on metabolization of tissue protein for maintenance energy (i.e., apparent starvation). Therefore, individuals transported on water currents to impinge on travelling screens may have been in relatively poor reproductive condition. Leaving the substratum to be carried passively downstream on water currents prior to spawning may be highly adaptive in these individuals if it allows migration to microhabitats more favorable to acquisition of food resources supporting gamete production. This hypothesis is supported by the observation that adult specimens of *C. fluminea* were only taken in high numbers from the travelling screens during periods preceeding incubation and spawning.

EMBRYOPHORE BROOD NUMBER, SIZE AND GROWTH IN RELATION TO MATERNAL AGE AND SIZE

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A population of the sexually-dimorphic freshwater prosobranch, *Viviparus georgianus,* in Tully Lake in central New York was regularly sampled between April, 1980 and July, 1982. Individuals are long-lived and iteroparous, becoming reproductively active during their second year. Ovoviviparous females have a maximum lifespan one year longer than that of males (4+ years as opposed to 3+ years in males). Potentially, females can produce annual broods for three consecutive years, spat being carried overwinter and released each spring. Juvenile mortality halves each cohort within the first three months and subsequent female survivorship is positively size-related. Female growth rates decline with age, and incremental growth within any year is positively correlated with individual size at the start of that year. Seasonal fluctuations in growth are exhibited by females, with somatic tissue growth declining during periods of reproductive activity and overwinter.

Female reproductive effort (R.E.) is positively age-related, increasing from 5.3% for modal 2-year females to 79.7% for modal 4-year females. However, due to the greater numbers of reproductive individuals and their large broods, 3-year females produce approximately 50.0% of any new cohort, with 2-year and 4-year females producing 21.0% and 26.0% respectively. In 2-year females, reproduction is restricted to snails > 16 mm S. L. In these animals, early reproduction does not appear to impose any significant survivorship penalties.

Spat and embryophore size are positively correlated with female age irrespective of female size. Brood numbers are positively correlated with maternal size and prebreeding growth-rates. In cage experiments, spat born early to older females and reared at low density grew fastest. Initial growth affects subsequent survivorship and age of first reproduction with the young of older females having greater lifetime fecundity and fitness. Therefore older females must contribute disproportionately to future reproductive generations in this stable, age-structured population.

INTERNATIONAL SYMPOSIUM: CLOSING REMARKS AND CONCLUDING SUMMARY (NORFOLK VIRGINIA, 1984)[1]

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If there is any generalization to be made regarding the twelve papers given in this symposium, it is that the field of physiological ecology as applied to freshwater molluscs is not only still a viable one, but also one of enormous potential for evolutionary studies. It may be worth spending a little time on semantics. We did all stick to molluscan examples, and to freshwater forms, with the exception of a few marine comparisons in the papers by Dr. Little and by me. However, there is greater difficulty in defining "physiological ecology." Recently, the Ecological Society of America took up most of an issue of their Bulletin with divergent views on the focus and extent of this subdiscipline. Last year, I stated in print (Russell-Hunter, 1983) that "As in the similar case of biophysics, for which different groups of scientists claim distinct missions, it may not be necessary or desirable to limit inquiry by strict definition of the field." At that time, I was editing a volume in which definitions of physiological ecology varied from author to author.

It remains important, as noted below, to carry the careful controls and factor analyses of good sound physiological work into the field. For our purposes, a broad semantic generalization can be used to go on with. It is that physiological ecology concerns those parts of the study of interrelations between organisms and environment, which are especially concerned with physiological mechanisms or are largely based on physiological measurements.

In these three sessions we have heard twelve papers that could be grouped in many ways. The alphabetic arrangement adopted by Drs. Burky and McMahon was probably wise. I shall take the greater risk of dividing them into five groups that run in a spectrum from the more physiological (process descriptive, reductionist) to the more purely ecological (system predictive, "holistic").

First, we considered water and ionic control in the prosobranchs and bivalves of fresh waters with the papers of Drs. Little and Dietz. In prosobranchs, studies of the functional morphology and ultrastructural organization of renopericardial structures can lead to a better understanding of the mechanisms on which high urine flow is based and to the conclusion that muscular pumping is of great importance. In bivalves, the ionic exchange during this great water flux involves neurohormonal controls, and we also heard about the dynamics of the unusual calcareous concretions in the gills, and the mineral supply provided for the fetal young. In broad, general terms these papers of Drs. Dietz and Little emphasized the extraordinary stresses faced by soft-bodied animals, lacking the waterproof cuticles of arthropods, nematodes and even fishes, in a medium with concentrations of inorganic salts two orders of magnitude less than those in the sea. Given the greatly increased surface:volume ratios of smaller organisms added to the lamellate gills of bivalves, it is extraordinary that such minute forms as Dr. Hornbach's *Pisidium* spp. can exist, far less exhibit the variety of metabolic and life-cycle parameters that they do.

Secondly, we considered the physiology of feeding, again in freshwater prosobranchs and bivalves, in the papers presented by Drs. Tashiro and Burky. Both sets of studies developed the ecological implications of differences in trophic input, particularly as related to the seasonal variations in freshwater environments. In the prosobranch *Bithynia,* the filter-feeding mechanism is energetically more efficient than the alternative grazing mechanism, resulting in a higher net gain of protein-carbon per respired costs. Capacity for particle size selection could have considerable ecological significance, suggesting a basis for interpopulation differences in preferred patterns of feeding. In *Musculium,* filtration rates differ when the clams are presented with suspensions of different particle concentrations, at different oxygen concentrations, and at different temperatures. These data reflect the sequence of seasonal and life-history changes for these clams. As pointed out, the central paradigm of ecological bioenergetics hinges upon ingestion rates. Many ecological models concerned with reproductive partitioning and tradeoffs assume either continued satiation of a single K-asymptote of trophic limitation. These studies emphasize the unreality of such modelling, when field conditions of seasonal variation are taken into account.

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[1] Note that the present text corresponds as closely as possible to the summary lecture itself, 25 July 1984.

Thirdly, we heard a group of papers concerned with seasonal variations in catabolic partitioning by Ms. Williams and Drs. McMahon and Aldridge. Two of these involved assessment of partitioning of protein-carbon and nonprotein-carbon by nearly simultaneous measurements of oxygen uptake and of nitrogenous excretion. All three papers reported respiration measurements, respectively in a pulmonate, a prosobranch, and a clam from fresh water. In an experiment set up by a Texas Power authority as a result of their discharge of heated effluent into one side of a dammed lake, heat adaptation was studied in *Physella virgata*. Although within about 70 generations, physiological races had apparently evolved in relation to upper thermal survivorship, this adaptation did not seem to have affected the temperature relationships of other physiological processes. Reversable respiratory acclimations to higher temperatures and to lowered oxygen tensions were also noted. In the prosobranch, *Leptoxis carinata*, the contributions of protein-carbon to catabolism and assimilation efficiencies differed in three populations but were highest during the summer. Nonprotein-carbon provides the majority of catabolism during fall and winter. In the invasive clam *Corbicula fluminea*, there is an apparent shift from largely nonprotein catabolism in winter to protein catabolism during the reproductive periods of summer and fall. Although current interest in *Corbicula* stems from the enormous costs and inefficiencies that can result from blockage of cooling lines and condensers (particularly hazardous in nuclear reactor cooling systems), these physiological studies point to a matter of considerable importance in ecological bioenergetics. In the studies presented here, and in others reported elsewhere by Drs. Aldridge, Buckley, McMahon, Payne, Tashiro and me, repeatedly there becomes manifest an energetic paradox, unreasonable to a Scots ecologist. It is that, at the very time when an appropriate parsimony of resources would require that the building blocks of protein be conserved for use in the reproductive output of eggs, there is increased burning of protein-carbon for catabolic purposes. Thus far, I have been unable to interest biochemist associates in any investigation of the putative molecular basis for this apparent ecological paradox.

Fourthly, we turned to consideration of overall actuarial bioenergetics in the two papers by Dr. Streit and me. Using the European freshwater limpet *Ancylus fluviatilis*, Streit's elegant experiments with ^{14}C-labelled algae demonstrated partitioning of assimilation into reversible and nonreversible pools. The relatively low net growth efficiencies in *Ancylus* with a slow accumulation of tissue growth may well be a characteristic of freshwater molluscs in less predictable environments. My review of data on molluscan tissue degrowth and its consequences stressed degrowth (decrease in structural proteins through time) as a dynamic process involving component rate changes. Capacity for controlled degrowth in flatworms and molluscs compels reconsideration of certain model systems in theoretical ecology, and also may have some phyletic significance.

Fifthly, we brought consideration of physiological differences in metabolism into focus as determinants of life-cycle pattern in freshwater molluscs. Using clams, pulmonates, and prosobranchs, respectively, Drs. Hornbach, Brown, and Buckley discussed the physiological and bioenergetic parameters which can constrain simpler fitness predictions regarding life-cycle variation within and between species. In a consideration of thirty-four populations of twenty-one species of pisidiid clams, variations in weight-specific metabolic rates affect turnover ratios and hence life-history parameters. For example, among *Pisidium* from softer waters lower metabolic rates correlate with smaller size at maturity and lowered fecundity. In *Lymnaea elodes*, growth rates and reproductive rates vary greatly between populations, but transfer experiments involving specially-reared F1 juveniles showed that considerable phenotypic plasticity occurs in life-history traits in this marginal species. Finally, the viviparous prosobranch, *Viviparus*, has been used in a field investigation of a classic problem in the ecological modelling of reproductive effort. This involved, for maternal snails, a convincing separation of age-related variation from size-related variation in fecundity, with differential levels of selective advantage for the offspring spat.

Clearly with this last group of papers, our studies in physiological ecology reach closest to the system predictive studies current in "pure" ecology. However, as physiological ecologists or field physiologists, we are driven to accumulate the best substantive data sets we can for comparisons in rate terms which can be particularly advantageous if computed into dimensionless index numbers (Russell-Hunter and Buckley, 1983). Relating such substantive data sets to the theoretical ecologists' models formulated in fitness units may not be easy. This should not deter us from our kind of investigations and experiments. A pluralistic approach to ecological problems cannot be sterile. From markedly different viewpoints, both Calow (1979) and Stearns (1980) have noted the need for more background knowledge of physiology in discussions of life-cycle evolution (see also Russell-Hunter et al., 1984). All hypotheses of evolutionary ecology—no matter whether initially developed in the field, in the laboratory, or at the computer—must subsequently revert to testing under field conditions, more specifically within the dynamics of naturally age-structured populations in their natural environment (Russell-Hunter, 1983).

Throughout all the diversity of the studies reported here, we have been looking quantitiatively at physiological variation involved in interactions of the mollusc with its freshwater environment, and with seasonal and other shifts in the abiotic and biotic constraints of that environment. When the distribution records of freshwater molluscs were first considered in descriptive ecology (for example, Boycott, 1936), it was obvious that hard, eutrophic waters had great species diversity as well as possibly greater molluscan standing crop biomass, but the causal factors, the "why" seemed unanswerable. Two decades later, a survey paper of my own (Russell Hunter, 1957) detailed the "how" of freshwater snail distribution in Scotland but still not the "why." We are now approaching a better quantification of the abiotic constraints of the distribution of freshwater molluscs which should allow a better definition of the framework for the biotic competition which was earlier proposed by one of our speakers (Brown, 1982). Obviously, our colleagues working on the ecology of littoral marine molluscs have already gone somewhat further in applying their findings to an understanding of community interactions and the dynamic equilibria of persistent zones (Lubchenco, 1978; Lubchenco and Menge, 1978; Menge, 1976).

One somewhat wry definition of physiological ecology by Fogg (1965) stated that it was "physiological work done under the worst possible conditions" in the field. This has considerable truth. I could reminisce about taking samples for microgasanalyses from mantle-cavities of snails in the cold waters of Loch Lomond more than three decades ago (Russell Hunter, 1953). Despite the trials of field investigations, it is important to ensure that the appropriate experimental controls (see, for example, Hurlbert, 1984) and restricted factor analysis parallel those of the best physiological work in the laboratory. Field encounters with populations (or cohorts) of molluscs that do *not* fit into accepted concepts of physiological optimality may be very important. In seeking evolutionary significance, my own prejudice is to look for suboptimalities in processes, as in an earlier biology morphologists were intrigued by vestigial organs (Russell-Hunter, 1983; see also Gould and Lewontin, 1979; Janetos and Cole, 1981; Mayr, 1983). Similarly, we have been impressed by anacoluthical series of adaptations where evolution has proceeded in discontinuous series not necessarily matched with each other (McMahon and Russell-Hunter, 1977; Mayr, 1983).

The evolutionary biologist who is sufficiently curious will always profit from a closer examination of unanticipated departures from optimality, and from the "out-of-step" adaptations of anacoluthical series. More generally, it is important to note that physiological work carried out on organisms such as molluscs from laboratory cultures can yield mean rate values for various physiological processes, and even relate these to changes in certain physical factors. However, only physiological studies based on natural populations of the same molluscs can establish the field range of individual variation in these rates—the range upon which natural selection operates to produce evolutionary change.

ACKNOWLEDGMENTS

First, we must all thank Dr. Robert Robertson, President of the AMU in this, its 50th year, both for the original idea for this symposium and for much logistical help in carrying it out. Secondly, the two organizers of the symposium, Drs. Albert J. Burky and Robert F. McMahon are owed a great deal of gratitude for detailed planning which extended over 18 months. Thirdly, we should recognize the efficiency of the three conveners of these sessions, Drs. Arnold G. Eversole, Barry S. Payne and Carl M. Way in keeping our presentations and discussions properly paced within the meeting schedules. Of course, the synergic properties of this series mostly derive from the continued coadjuvancy of Drs. Burky and McMahon from time past through time future. Particulary over the last six months, the notices issued, letters written and telephone calls made by Dr. Burky to bring us together must number into the hundreds. Similarly, over the next few weeks, Dr. McMahon will be much concerned with the written versions of our presentations and with ensuring that Dr. Robert S. Prezant can hold to his appropriately high editorial standards while publishing much of our symposium. It gives me particular pleasure, both personally and fraternally, to use this opportunity also to thank Dr. Prezant for his help.

During the introductory remarks by Dr. McMahon yesterday and Dr. Burky today, and while this symposium progressed, I felt more and more like Samuel L. Clemens—and must state publicly that rumors of my imminent retirement and old age have been greatly exaggerated. I remain very grateful to Dr. McMahon and the others who have suggested that my own research work *does* have a continuing future. It is true that I shall be 60 in less than two years. It is true that my first doctoral graduate student has just retired. It is true that 40 years ago this month, I first looked closely at *Ancylus*. However, I hardly think these truths justify the Royal Society of Edinburgh in importuning me (as they have been doing) to produce material for my obituary file. As I said, I hope the rumors are exaggerated. I must thank you all for attending and contributing to this signal symposium.

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CONTRIBUTOR INFORMATION

The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research and detailed reviews dealing with molluscs will be considered for publication.

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Beattie, J. H., K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters (*Crassostrea gigas*) during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184–189.

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